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Effects of natural and anthropogenic forest edge on songbirds
breeding in the boreal mixed-wood forest of northern Alberta

by

Samantha Jane Song ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of
the requirements for the degree of Doctor of Philosophy

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Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled "The effect of natural and anthropogenic forest edge on songbirds breeding in the boreal mixed-wood forest of northern Alberta" submitted by Samantha Jane Song in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Abstract

Current harvest designs for logging in the boreal mixed-wood forest will result in the conversion of Alberta's relatively continuous forest cover to a patchy mosaic of clearcut and uncut forest blocks. Research was undertaken to determine how songbirds respond to the creation of forest edge by logging. Negative effects of edge on songbirds, especially increased predation of eggs and nestlings at the forest edge vs. the interior, have been implicated in the decline of songbird populations across North America.

In northern Alberta, the forest is a natural mosaic of stands of conifer and aspen (*Populus tremuloides*) and a large amount of forest edge is already present. Therefore, I compared songbird communities at forest/clearcut edges with both the forest interior and natural edges to provide a more realistic context for effects observed at anthropogenic edges. I measured density and species composition of songbird communities, predation on artificial nests, food supply and vegetation structure for 2 years at the following sites: (1) aspen adjacent to 1-2 y old clearcuts, (2) aspen adjacent to white spruce stands, (3) interior of aspen stands. In the predation study, I included aspen adjacent to seismic lines as an additional treatment.

Forest/clearcut edge did not have a strong effect on songbird communities compared with other edge types. Density of songbird communities at aspen/clearcut edge was higher in the first year post-cut than at aspen/white spruce edge and the forest interior but this difference disappeared in the second year post-cut. This temporary increase in songbirds at the clearcut edge was likely caused by crowding of birds displaced from clearcut areas. Predation on artificial nests at aspen/clearcut edge was not higher than levels observed at other sites. Invertebrate biomass was affected by edge type in some cases but did not relate to songbird response to edge. Vegetation structure, particularly stand age, canopy cover, understorey density and amount of conifer, was important for predicting density and composition of songbird communities in aspen stands. Besides mitigation of habitat loss, management of adequate rotation length and ratio of deciduous/coniferous mix in stands may be more critical for maintaining songbird populations than limiting forest edge.

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Chapter 1: Introduction to edge effects on songbirds breeding in the boreal mixed-wood forest.

1.0 Introduction

An edge, a junction between two communities, can have beneficial and adverse affects on wildlife and thus, whether to advocate or discourage the creation of edges has been a source of controversy for wildlife managers (Harris 1988, Reese and Ratti 1988, Yahner 1988, Hunter 1990). Historically, the term edge effects has referred to the tendency of plant and animal diversity to increase at the edge of two habitats (Leopold 1933, Alverson *et al*. 1988). However, the work of Gates and Gysel (1978) marked the beginning of a change in attitude by biologists towards the impact of edges on wildlife. In their work, densities of nesting songbirds increased at the edge of forests adjacent to fields, a response attributed to the availability of habitat suitable for nesting and foraging. Productivity of these birds was low though, because breeding birds experienced high levels of cowbird parasitism and predation on eggs and nestlings. The edge, it seemed, acted as an "ecological trap" for songbirds.

Since the seminal work by Gates and Gysel (1978), research on edge effects on songbirds has proceeded at a rapid rate, spurred by the increasing rate of habitat fragmentation caused by anthropogenic activity and a concurrent decline in songbird populations in North America (Sauer *et al*. 1997). Habitat fragmentation that results in negative edge effects, reduced patch area and increasing isolation of populations, in conjunction with habitat loss, has had a major impact on songbird populations by increasing local rates of extinction (Whitcomb *et al*. 1981, Terborgh 1989, Robinson *et al*. 1995). Many studies have targeted the effects of edge on the pattern of songbird communities or on individual processes such as nest predation or parasitism that may affect the pattern of songbird communities at edges. However, fewer studies have taken an integrative approach to understand how songbirds respond to an edge, which factors affect their response and how edge can influence processes that affect songbird success.

The boreal mixed-wood forest of northern Alberta presents a unique opportunity to study the effects of edge on songbirds. It is a highly heterogeneous landscape that covers

more than half of Alberta's land base (Strong 1992). Due to natural variation in topography and a history of natural disturbance from fire and insect outbreaks, it is composed of deciduous and coniferous stands as well as wetlands, bogs, lakes and rivers (Peterson and Peterson 1992). Birds comprise 72% of all vertebrates in this region (Smith 1993) yet we know surprisingly little about their dynamics here (Schmiegelow and Hannon 1993). Until recently, there has been little history of timber harvesting in the boreal forest. In the last decade, the government of Alberta has moved to exploit this resource and, currently, 195.662 km^2 of Alberta's boreal forest are leased to forestry companies (D. Price, Alberta Environmental Protection, pers. comm.). Clearcut harvesting leaves an alternating pattern of cut and uncut forest blocks; therefore, anthropogenic edge is imposed across a system that already has an extensive amount of natural edge. If edges induced by clearcutting act as an ecological trap for boreal birds, the impact will be far-reaching.

Although the effect of natural edges on songbirds has been noted as an important area for future research (Paton 1994), studying natural edges when trying to understand the effect of anthropogenic edges in this system serves another important function. Most studies on edge effects compare conditions at the edge with the interior, with the interior representing natural or normal conditions for songbirds (e.g. Gates and Gysel 1978, Helle and Helle 1982, Wilcove 1985, Lovejoy *et al.* 1986, Darveau *et al.* 1997, de Casenave *et al.* 1998). Due to the natural heterogeneity of the boreal landscape, using both the forest interior and natural edges provides a more realistic picture of the natural range of habitats that birds can encounter, and thus, provides a stronger context for the assessing the impact of an anthropogenic edge.

This study was designed to determine the response of songbird communities to an anthropogenic edge, a natural edge and the forest interior. I also examined factors that could affect songbird success, specifically, predation, availability of food and vegetation structure. Although many studies have individually examined the effect of edge on density, diversity and/or richness of songbird communities and the effect of edge on nest predation, no studies have attempted to integrate the effects of edge on songbirds, their predators,

their food and their habitat within one system. As recently pointed out by Robinson (1998), studies of fragmentation effects on birds have often neglected the link between birds and their food supply. Including this component provides a clearer picture of the dynamics of songbirds at edges.

Within this thesis, I have addressed a range of problems concerning songbirds at edges in the boreal forest. I have defined "edge" as the junction between two diverse communities including the junction of different forest stand types. In Chapter 2, I determined whether the response of songbird communities differs between natural and anthropogenic edges and the forest interior. I also examined the role that vegetation plays in this response. In Chapter 3, I investigated the response of invertebrates to natural and anthropogenic edges and the forest interior and determined if songbird densities are related to invertebrate biomass. In Chapter 4, I looked at the relative predation pressure on songbird nests between natural and anthropogenic edges and the forest interior using an artificial nest design. In my final chapter, I have provided a synthesis of all my results and comments on their implications for songbirds in an industrial forest landscape. Finally, I have presented some directions for future research and management recommendations for timber planning.

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Chapter 2: Songbird response to natural and clearcut edges in the boreal mixed-wood forest.

2.0 Introduction

The edge, the junction between two communities, can affect the composition and abundance of songbird communities (see Table 2.1 for review). Although the effect is not consistent among all studies, songbird density and species richness are often higher at edges than in the interior, particularly for forest edges created by habitat removal during anthropogenic disturbances such as industrial forestry or agriculture. Species composition can also change at the forest edge: some species are found mainly at the forest edge while others avoid the edge and remain in the interior (Johnston 1947, Whitcomb *et al.* 1981, Yahner 1988, Rich *et al.* 1994). The forest edge can act as a settlement boundary if habitat conditions beyond the edge are unsuitable (Hunter 1990) and it can also act as a source of habitat loss if some species of birds avoid using the edge entirely. Further, songbirds breeding at forest edges can experience high rates of nest predation and parasitism (Gates and Gysel 1978, Brittingham and Temple 1983, Gates and Giffen 1991) and increased competition (Ambuel and Temple 1983, Hagan *et al.* 1996), and this may intensify the contribution of forest edge to habitat loss. The creation of habitat edge along with other effects of habitat fragmentation, i.e. reduced patch area and increased isolation of populations, has been implicated in the decline of neotropical migrant birds in parts of North America (Whitcomb *et al.* 1981, Sauer and Droege 1992, Robinson *et al.* 1995, Kirk *et al.* 1997).

The extensive body of research on edge effects provides a basis for predicting when density and species composition of songbird communities will differ between the edge and the interior of a forest. Many studies show that density and species composition of songbird communities can be predicted by vegetation structure, specifically vertical heterogeneity, i.e. the complexity of the foliage profile within a stand (MacArthur and MacArthur 1961, Karr 1968, Recher 1969, Willson 1974, Collins *et al.* 1982, Freemark and Merriam 1986, DeGraaf *et al.* 1998). Vegetation at the forest edge, especially at edges formed by clearings, often increases in vertical heterogeneity over time because the

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increase in light at the edge allows the shrub understorey to develop (e.g. Ranney *et al*. 1981, Fraver 1994). If this occurs, abundance and species richness of songbird communities also tends to increase at the edge compared to the interior (e.g. Anderson *et al*. 1977, Gates and Gysel 1978, Strelke and Dickson 1980, Helle and Helle 1982, Kroodsma 1984a, Elliott 1987 but see Lovejoy *et al*. 1986). In many studies, species in communities have been categorized as "edge" and "interior" species depending on where they are most often observed (e.g. Johnston 1947, Whitcomb *et al*. 1981, Robbins *et al*. 1989, de Casenave *et al*. 1997). Often, "edge" species are those that are attracted by areas of high vertical heterogeneity e.g. shrub-nesting species, while "interior" species may avoid these same features (Freemark and Merriam 1986). If vegetation structure is the main factor affecting songbird settlement, species specific to the stand edge or interior would only be expected in forests where vegetation structure differs between the edge and the interior of a stand (Hansson 1983).

Both edge contrast and ecotone width are potential predictors of differences in songbird density and community composition between patch edge and interior. Edge contrast is a measure of structural similarity between the two ecosystems forming an edge (Thomas *et al*. 1979) and ecotone width is a measure of the transition from one ecosystem to another (Hunter 1990). Contrast is an inconsistent predictor of edge effects on songbird densities (e.g. Elliot 1987, Small and Hunter 1989). Contrast and ecotone width may be better predictors of edge permeability (*sensu* Weins *et al*. 1985) than of songbird densities. Low contrast edges with wide ecotones (graded edges) have vegetation species and characteristics from both habitats and they may provide habitat for species from both adjacent ecosystems (Hunter 1990). Therefore, species may be more likely to utilise both sides of the edge, i.e. a graded edge may be less likely to act as a settlement or habitat boundary for birds. Accordingly, for forests adjacent to clearings, graded edges may facilitate invasion of the forest by birds associated with the adjacent habitat and increase competition for forest-dwelling species (e.g. Ambuel and Temple 1983). Few other studies have compared abrupt and graded edges to determine their relative effect on species richness and songbird settlement (e.g. DeGraaf 1992).

The boreal mixed wood forest of Alberta is a relatively unknown system (Schmiegelow and Hannon 1993, Schmiegelow *et al.* 1997) that has been targeted for aggressive development (Pratt and Urquhart 1994). Harvesting of aspen (*Populus tremuloides*) stands has recently been initiated across the northern half of the province. Logging results in a checkerboard pattern of cut and uncut stands and the creation of large amounts of forest/clearcut edge. A negative effect of forest edge on songbird communities could exacerbate the habitat loss caused by clearcutting. Historically, the boreal forest has been disturbed by fire and insect outbreaks (Peterson and Peterson 1992) so there may be some adaptation to edge by birds (Hunter 1992). The landscape itself is a patchy mosaic of aspen, spruce, bogs and wetlands so other types of forest edge are a dominant feature here.

Most of the studies of songbird response to forest edge have been conducted in forest adjacent to clearings but there are no studies that have examined the effect of edge adjacent to very recent (≤ 2 years) clearcuts (see Table 2.1). For this type of edge, vertical heterogeneity at the edge may not be the only factor influencing songbird density and species composition. Habitat removal by clearcutting can cause displacement of birds and result in an increase in density or "crowding effect" in the adjacent forest in the short term (Whitcomb *et al.* 1981). In previous studies, crowding has been associated with smaller forest patches (Darveau *et al.* 1995, Hagan *et al.* 1996, Schmiegelow *et al.* 1997).

This study was designed to determine the effect of different types of forest edge on songbird communities. Density, richness and species composition of songbird communities at clearcut edges were compared to both the forest interior and a natural edge consisting of aspen adjacent to white spruce. The natural edges were typically much more graded (wide ecotone, low contrast) than the abrupt (no ecotone, high contrast) clearcut edges.

Studies on forest edge and songbirds tend to compare songbird communities at the edge to the forest interior because the interior represents the "control" or "status quo" habitat for songbirds. This approach is clearly inadequate for assessing the impact of clearcut edges on songbirds in the boreal forest because the forest encompasses a range of habitats in its natural state. Including a natural edge in this study provides a broader

understanding of the natural variation in habitat that songbirds experience within the boreal forest and thus, a stronger basis for my conclusions concerning the effect of anthropogenic edge. In addition, studies on natural edges are few and no studies have examined the types of natural edges found in the boreal forest.

Specifically, I addressed the following questions in this study:

(1) Does density, species richness and composition of songbird communities differ between anthropogenic edges, natural edges and the forest interior?

(2) Is a graded natural edge less likely to act as a habitat boundary than an abrupt anthropogenic edge?

(3) Are individual species level responses the same as the community level response?

(4) Are there "edge" and "interior" species in the boreal forest, i.e. are there species that are only found at the edge or in the interior?

(5) At a particular edge type, are there songbirds that are attracted to or avoid the forest edge?

(6) Do songbird species introduced by the creation of clearcut habitat invade across the forest edge, i.e. are they a possible source of competition for forest species?

(7) Do other factors, such as stand heterogeneity and vegetation structure and species composition, predict songbird densities and patterns of songbird communities more effectively than forest edge?

(8) Will edge effects change as clearcuts regenerate?

2.1 Methods

2.1.1 *Study area*

The study was conducted over 2 years (1995-96) in north-central Alberta, Canada, near Calling Lake (UTM Zone 12: 344214 E, 6133569 N) in boreal mixed-wood forest (Figure 2.1). Forested areas are dominated by trembling aspen, *Populus tremuloides,* balsam poplar, *Populus balsamifera*, and white spruce, *Picea glauca*, on upland sites (Strong 1992). Wetter sites are characterised by black spruce, *Picea mariana,* and willow,

Salix spp. Major understorey species in aspen stands include: green alder, *Alnus crispa*, low-bush cranberry, *Viburnum edule*, prickly rose, *Rosa acicularis*, beaked hazelnut, *Corylus cornuta*, bracted honeysuckle, *Lonicera invulcrata*, and willow, *Salix* spp. Wild sarsaparilla, *Aralia nudicaulis*, dewberry, *Rubus pubescens*, fireweed, *Epilobium angustifolium*, bunchberry, *Cornus canadensis*, and various grasses (e.g. *Calamagrostis canadensis*) are commonly found in the herb layer. White spruce stands have a very short, low understorey. Dominant species include: wild sarsaparilla, bunchberry, dewberry, grasses, twinflower, *Linnea borealis*, Labrador tea, *Ledum groenlandicum*, and various mosses (e.g. *Lycopodium annotinum, Pleurozium schreberi*).

Sites were distributed over four contiguous 10 x 10 km townships. Clearcutting of aspen stands in a portion of this area was conducted in the winter of 1993 and summer of 1994. Clearcut blocks alternated with uncut blocks and averaged 25 ha in size. There is no large scale history of deciduous logging in this region (Strong 1992). No site preparation took place on the blocks after harvest. Conifer clearcutting was also conducted in this region in the winter of 1993, followed by blade scarification; these blocks were not included in this study. Approximately 8% of the terrestrial landbase was harvested and aspen and spruce stands make up another 67% of that landbase. Clearcuts were covered by low vegetation (<1 m in height) consisting primarily of aspen and balsam poplar suckers, green alder and grasses and coarse woody debris (tree tops and limbs left over from logging operations).

2.1.2 *Songbird surveys*

Density and composition of songbird communities at each type of edge was assessed by spot-mapping of male's territories from late May through June, i.e. when birds are settling onto territories until nestlings fledge (Verner 1985, Ralph *et al.* 1993). Although spotmapping is more time-consuming than conducting point-counts, I chose this method because spot-mapping provides (1) stronger evidence that birds are holding territories, (2) clearer information about territory location, and, (3) better estimates of density (Bibby *et al.* 1992). The timing of surveys focused mainly on monitoring migratory species and

excluded most resident species. Approximately 5 ha survey grids were established in: (1) the interior of aspen stands, (2) aspen stands adjacent to 1-2 year old clearcuts, and (3) aspen stands adjacent to old (>110 y) white spruce stands. Each grid followed the forest edge for 250 m and extended 150 m into the aspen habitat and 50 m into the adjacent habitat (Appendix 2.1). (In interior sites, the entire grid was in aspen). I used 6 grids/treatment in the first year and 8 in the second (Appendix 2.2). In each treatment, there were mature and old aspen stands, with an average age of stand origin of 1920 and 1870, respectively. These stands reflected the average age of aspen stands in this region. In 1995, I used 2 mature and 4 old stands in each treatment and in 1996, I added 2 more mature stands to each treatment. In both year, aspen stand sizes ranged from 16 to 443 ha with a mode of 115 ha. Sites were selected so that each treatment had edges facing a full range of aspects (all major cardinal directions).

Grids were censused in fine weather by walking slowly along the transects laid parallel to the edge and 100 m into the aspen, and recording the species and location of singing males. Route direction and observers were alternated each visit. In each year, 3 observers surveyed the grids and 1 observer was constant between years. Observers walked each grid such that survey time was equally allocated throughout the grid. To help define territories, we recorded additional information about songbird activity such as countersinging, calling, aggressive encounters, nest locations, carrying nest material or food. Censusing was conducted from dawn until 10 a.m., when avian activity is highest. Spot-mapping grids were censused approximately every 5-6 days, weather permitting, for a total of 6 rounds in 1995 and 7 rounds in 1996. Territories were defined by clustered records of singing males where a cluster had at least 2 records 10 days apart (Bibby *et al*. 1992). Territories that lay over a grid boundary and had equal registrations in and out of the grid were counted as half territories but no further subdivisions of territories took place.

Red-eyed Vireo was not reliably distinguished from Philadelphia Vireo by observers; therefore, I lumped these 2 species. Point count studies in the area indicate that Philadelphia Vireo was approximately 15 times less abundant that Red-eyed vireo

(Schmiegelow *et al.* 1997). Nomadic species that travelled in flocks e.g. Pine Siskins, *Carduelis pinus*, and Cedar Waxwings, *Bombycilla cedrorum*, were excluded from the analysis.

2.1.3 *Vegetation sampling*

Vegetation structure and species composition were recorded within each spotmapping grid using 0.04 ha plots and a protocol modified from the BBIRD program (Martin 1992). Within a grid, 3 transects were established 100 m apart and perpendicular to the edge (Appendix 2.1). Along each of the 3 transects, a plot was placed (1) at a random distance from the edge between 5-50 m, (2) at 100 m and (3) at 150 m from the edge. Two additional plots were placed in the 5-50 m zone between transect lines such that vegetation plots were 50 m apart here (see Appendix 2.1 for layout). Records from all 11 plots were averaged for each grid. In 1996, I sampled vegetation at the edges of 8 aspen stands next to 15 year old clearcuts. In each stand, 5 plots were placed 50 m apart and at a random distance from the edge into the unharvested aspen between 5-50 m.

Within each vegetation plot, the number, species and diameter at breast height (DBH) of trees and snags were recorded. Snag height was also recorded. Within a 0.008 ha nested sub-plot, number and species of saplings (DBH<2.5 cm) and poles (DBH 2.5-8 cm) were measured. Plots were divided into 4 quadrants, such that the dividing radii were perpendicular or parallel to the edge. At the 5 m point along each radius, using a 1 m^2 quadrat, data were collected on: ground cover (% of all green, shrub, forb, coarse woody debris, grass, dead grass and moss cover), and shrubs (number and species). Along each radius, number, diameter and length of coarse woody debris (CWD) were recorded. At each plot, average canopy height was recorded using a clinometer and canopy cover was measured using a densiometer.

Information on fine-scale horizontal heterogeneity of the spotmapping grid was collected by individual observers mapping each grid on the ground. Observers recorded location and size of white spruce clumps and major canopy gaps (e.g. gaps due to wet areas, seismic lines (8 m wide corridors cut for oil and gas exploration), etc.). The

resulting maps were scanned into IDRISI, a geographic information system (Eastman 1997), and the edge:area ratio of all patches was calculated. By averaging edge:area ratios and dividing by grid area, an index of heterogeneity was generated for both spruce patches and major canopy gaps within each grid.

Stand area and age were recorded from Alberta Vegetation Inventory or Phase 3 Forest Inventory maps.

2.1.4 *Statistical Analysis*

Analysis of variance (ANOVA) was used to compare territory density and species richness between edge types. Data were log-transformed to ensure homogeneity of variances. Alpha was set to 0.10 because failing to reject the null hypothesis in this study when it is actually false could have negative implications for songbird conservation. Means are reported ± standard error and power is reported for $\alpha=0.10$. When either power was low (≤ 0.65) and when effect size was large ($d>0.2$) (Cohen 1988), my ability to detect a statistical difference was low. In these cases, I used a randomization technique to verify the results of the ANOVA for each year and between years. I used the computer program RANDCOMP 0.1 (Brzustowski 1997) which generates a statistical distribution of differences between treatments by repeatedly sampling from the observed data set. The program then tests the observed difference between the means of two treatments against the generated distribution of differences. If the fraction of the random distribution of differences that is greater than the observed difference is ≤ 0.10, then the observed difference is significant (at $\alpha \leq 0.10$). The program was designed to test 2 groups; therefore, when I analysed the effect of edge, for each year, I performed 3 tests to compare all 3 treatments. I then adjusted the level of significance for multiple comparisons from $\alpha= 0.10$ to 0.02 (Zar 1984: p. 163). Because this method is awkward for reporting results, I showed only the results of the ANOVA. But, in no case did the randomization refute the conclusions determined by the ANOVA.

Cluster analyses were used to determine whether songbird communities were distinct to each edge type in each year. Mean territory density of each species was clustered using

the Phi-square method for count data and Ward's method of hierarchical cluster analysis (Norüsis 1994: Chapter 3).

Analysis of variance was used to determine the effect of edge type on the territory density of individual songbird species. Territory density between aspen and adjacent habitat were compared using analysis of variance or Mann-Whitney U-tests when assumptions for parametric analyses were not satisfied after transformations. Species with only one documented territory in a given year were eliminated from analyses. For species for which power to detect a difference was low ($1-\beta \leq 0.65$) and effect size was large ($d > 0.2$) (Cohen 1988), I used a randomization technique described above.

To determine whether birds in aspen avoided or were attracted to clearcut or white spruce edges in a given year, I compared the observed number of detections in 50 m zones of the grid, i.e. 0 to 50 m, 50-100 m and 100-150 m away from the edge, to a theoretical distribution of detections using a Kolmogorov-Smirnov (K-S) goodness-of-fit test. For species that were not significantly higher on the aspen side of the edge, I assumed that the theoretical distribution of detections was equal between zones. For species that were significantly higher on the aspen side of the edge, i.e. those that perceived the edge as a habitat boundary, the probability of detection could have dropped near the edge due to territory geometry, i.e. a smaller area of the circle was next to the edge and thus, fewer detections were registered (Kroodsma 1984b). To calculate this theoretical distribution, I assumed that territories were roughly circular and non-overlapping and that birds were equally likely to be detected throughout their territory. Using average territory density per grid, I calculated approximate territory area for each species and the amount of area covered by circles of the same area in each zone. Using this calculated territory size and the average number of detections/territory of each species, a theoretical distribution of the number of detections for each zone was generated for use in the K-S test. I did not include species that were detected fewer than 15 times in a treatment each year because my ability to detect significant differences was low below this level.

Stepwise multiple regression was used to test the effect of stand characteristics on songbird density. From the large number of variables generated from the vegetation plots,

the data set was reduced by replacing variables that were highly correlated (r>0.7) with a single representative variable. Linear regressions were run on individual variables and those with low explanatory power ($R^2 < 0.05$) in both years were eliminated from the analysis. Variables were (x+1) log-transformed or arcsine square root-transformed where necessary to achieve a normal distribution. The following variables were entered: dummy variables for each edge type, gap heterogeneity, conifer heterogeneity, # conifer poles, # deciduous poles, volume of CWD > 12 cm DBH, % green ground cover, shrub density and either stand age or canopy cover. Stand age and canopy cover were negatively correlated in both years but especially in 1995 (r=-0.7849). I included canopy cover and not stand age in the regression model because it resulted in a stronger (more significant slope, higher R^2) model.

Ordination analyses were performed using CANOCO 3.12 (ter Braak 1991) to examine the effect of vegetation structure on the composition of songbird communities. Selection of the appropriate technique was determined using a detrended correspondence analysis to test the unimodality of the data (ter Braak 1995). The gradient length of the first axis was approximately 2 standard deviations in both years, therefore either redundancy analysis (RDA), a linear technique, or canonical correspondence analysis (CCA), a unimodal technique, was suitable. RDA produced a better fit based on the amount of explained variance in the species densities and the explained variance in the fitted species data (ter Braak 1994). Vegetation variables as well as dummy variables representing each edge type were entered into the RDA. Variables were standardized to mean zero with a standard deviation of 1 and highly collinear terms were eliminated from the analysis. The vegetation variables used in the final model had significant canonical or regression coefficients based on their t-values for at least one of the first 2 axes and they also had the highest inter-set species-vegetation correlations (ter Braak 1995).

Vegetation characteristics between treatments were compared using one-way ANOVA's and Scheffé's post-hoc tests were performed on significant relationships (Day and Quinn 1989). Only data from all grids in 1996 were used because this year had the largest number of replicates and measures in aspen next to 15 y old clearcuts were also

taken in 1996. Variables were log-transformed, or arcsine square root-transformed for percents, to ensure normality. Measurements represent averages for each grid.

2.2 Results

2.2.1 *Effect of edge on songbird communities*

Territory density was not significantly different between edge types in either year (ANOVA, Edge: $F=1.57$, $p=0.222$, $1-\beta=0.44$, Year: $F=2.10$, $p=0.156$, $1-\beta=0.41$, Edge*Year: $F=1.00$, $p=0.379$, $1-\beta=0.32$, Figure 2.2). Similarly, there was no change in the species richness of those communities among treatments or years (ANOVA, Edge: $F=0.05$, $p=0.955$, $1-\beta=0.11$, Year: $F<0.01$, $p=0.988$, $1-\beta=0.12$, Edge*Year: $F=0.97$, $p=0.388$, $1-\beta=0.31$, Figure 2.3).

There was no effect of edge type on territory density of birds classified by migratory, nesting or foraging guild (Table 2.2). Densities decreased significantly between years though for short distance migrants (from (mean ± SE) 1.01 ± 0.14 to 0.59 ± 0.07 terr./ha), shrub nesters (from 2.35 ± 0.46 to 1.37 ± 0.25 terr./ha) and ground-gleaning species (from 1.59 ± 0.11 to 1.08 ± 0.09 terr./ha).

Cluster analysis did not group songbird communities by edge type. In both years, sites tended to be distinguished by the age and structure of the stand rather than the type of habitat that was adjacent to the stand. In 1995, sites clustered into mainly mature or older aspen stands with little shrub understorey and old aspen stands with heavy shrub understorey (Figure 2.4a). In 1996, sites clustered into mainly mature aspen stands and old aspen stands (Figure 2.4b), with the former cluster breaking into old aspen and old aspen mixed with mature white spruce and the latter cluster breaking into mature aspen with some white spruce understorey and mature or older aspen stands with little shrub understorey.

2.2.2 *Effect of edge on individual species*

Comparisons of territory densities for individual species generally reflected community level results (Figure 2.5). In 1995, 28 species held territories in aspen. Data from seven of these species were not analysed due to low densities. Of the remaining 21 species, 5 showed a change in density at an edge that differed from other treatments and for 4 of these species, the effect was at aspen/white spruce edge. Densities of Red-eyed Vireo and Warbling Vireo were both lower at aspen/white spruce edges than either interior or aspen/clearcut edges. Density of Black-throated Green Warbler was higher at aspen/white spruce edges than aspen/clearcut edges and density of Western Tanager was higher at aspen/white spruce edges than in interior sites. Only Canada Warbler showed a significant density increase at clearcut edges in 1995. In 1996, 32 species had territories in aspen of which 8 species were not analysed due to low densities. Seven of the remaining 24 species, showed an edge effect and again the response was to aspen/white spruce edges. Red-eyed Vireo, Warbling Vireo, Hermit Thrush and Rose-breasted Grosbeak had lower densities at aspen/white spruce edges while Western Tanager, Golden-crowned Kinglet and Dark-eyed Junco had higher densities at aspen/white spruce edges than both the interior and aspen/clearcut edges.

No territorial species were unique to the interior grids in both years (Figure 2.5). Western Wood-Peewee was unique to aspen next to clearcuts in both years although numbers were very low (2 territories in 1 grid in 1995 and 0.5 territory in 1996, both in the same grid) (Figure 2.5). Two species were unique to aspen next to white spruce although again, abundances are low: Dark-eyed Junco (0.5 territories in 1 grid in 1995, 2.5 territories over 3 grids in 1996) and Magnolia Warbler (1 territory in 1 grid in both 1995 and 1996 although different grids between years) (Figure 2.5).

The creation of clearcuts introduced new species: Alder Flycatchers, Tree Swallows, American Robins, Common Yellowthroats, Clay-coloured Sparrows, Lincoln Sparrows, and Swamp Sparrows all established territories in the clearcuts (Figure 2.6b, d). LeConte's Sparrows were also detected but were not abundant enough to determine whether they were territorial. None of these species had territories in the adjacent aspen habitat except

for American Robin where one territory in one grid straddled the edge. Half of a Common Yellowthroat territory was in one control site, but this was probably due to the presence of a nearby creek. These open area species are not invading the adjacent forested habitat (Figure 2.6).

No species were unique to the white spruce portion of the aspen/white spruce grids (Figure 2.7).

2.2.3 *Edge as a habitat boundary*

The clearcut edge acted as a habitat boundary for many species. For birds that held territories in aspen stands, 65% of 20 and 23 species in 1995 and 1996, respectively, had significantly lower densities or no territories in the adjacent clearcut (Figure 2.6). White spruce was a much more permeable edge with species tending to use both habitats. The territory density of 69% of 16 species in 1995, and 47% of 17 species in 1996, was not different between aspen and adjacent white spruce (Figure 2.7). Densities within the 50 m of adjacent habitat may be inflated compared to those in aspen stands because a much smaller area was sampled.

2.2.4 *Edge attraction and avoidance*

Within grids at clearcut edges, Least Flycatchers, Red-eyed Vireos, Tennessee Warblers, and American Redstarts were detected significantly more often than expected at 0-50 m from the edge in both years (Table 2.3, Appendix 2.5). Warbling Vireo and Rose-breasted Grosbeak were also detected in this range more often than expected but I had insufficient data to determine if this occurred in both years. For remaining 7 species that I tested, the distributions of observed detections either did not differ from expected or else differences between observed and expected distributions were not consistently different in both years. Although both Mourning Warbler and White-throated Sparrow use the clearcuts, neither species was consistently attracted to the edge. In fact, in 1995, Mourning Warbler was detected more often than expected in the 100-150 m zone.

In grids adjacent to white spruce stands, none of the 10 species tested was attracted to that edge type in both years (Table 2.3, Appendix 2.6). Both Red-breasted Nuthatch and Connecticut Warbler were detected more often than expected 0-50 m from the edge but sufficient data were only available for analysis in one year. Although territory densities of Western Tanager were significantly higher in white spruce than in aspen in both years, the observed distribution of detections within aspen was not different from random. Conversely, Yellow-rumped Warbler had higher densities in white spruce than in aspen in 1996 and it was also attracted to the aspen/white spruce edge in that year. Only White-throated Sparrow was shown to avoid aspen/white spruce edges in 1995; however, in 1996 this response was reversed and White-throated Sparrows were detected more frequently than expected 0-50 m from the edge.

2.2.5 *Determinants of density and community composition of boreal songbirds*

In 1995, the density of territorial songbirds increased at aspen/clearcut edges and with decreasing canopy cover (Table 2.4). In 1996, the edge effect was not present. Songbird density increased with increasing gap heterogeneity, and number of deciduous poles, and with decreasing canopy cover.

In both years, the structure or pattern of songbird communities in aspen stands was most strongly predicted not by edge type but by factors related to stand age, understorey complexity and stand species composition (Figure 2.8). The same four vegetation characteristics best described patterns in songbird communities in aspen stands in both years: stand age, basal area of conifer trees, canopy cover and number of deciduous poles (Figure 2.8). The canonical coefficients and intra-set correlations in Table 2.5 show that the first axis describes an age/stand complexity gradient, ranging from mature stands with simple understories to older stands with a complex understories. I generalise from stand age and deciduous poles to understorey complexity because (1) deciduous poles tend to reflect an increase in alder understorey, (2) deciduous poles are also positively correlated with variables such as volume of large snags (r=0.7658), deciduous saplings (r=0.5220), and volume of large CWD (r= 0.5663) and (3) the analysis below shows that older stands

tend to be more structurally complex (Table 2.7). The second axis describes a species composition gradient, ranging from pure aspen stands to stands with an increasing conifer component (Table 2.5).

In 1995, the eigenvalues for the RDA were 0.382 for Axis 1 and 0.117 for Axis 2. The biplot explains 49.9% of the variance in territory density of songbirds and 89.0% of the relationship between species and vegetation. In 1996, the eigenvalues were 0.304 for Axis 1 and 0.102 for Axis 2. Here, the biplot explains 40.6% of the variance in songbird densities and 89.2% of the relationship between species and vegetation.

Least Flycatchers, Western Wood-Peewees, Warbling Vireos, Yellow Warblers, Mourning Warblers, American Redstarts, White-throated sparrows, Rose-breasted Grosbeaks and, in 1995, Chipping Sparrows, are very closely associated with Axis 1 and the arrow for deciduous poles (Figure 2.8). Within aspen stands, these species tended to be found in older stands with a heavy alder understorey. Winter Wrens, Tennessee Warblers and, in 1996, Chipping Sparrows, were found in older stands with some conifer. Ovenbirds, Connecticut Warblers and Hermit Thrush were associated with mature stands with closed canopy cover and low understorey. Red-breasted Nuthatch, Swainson's Thrush, Yellow-rumped Warbler, Black-throated Green Warbler, Blackburnian Warbler held territories in stands with a higher conifer component. Alternatively, Red-eyed Vireo was found in stands with a very low conifer component. Habitat associations are not clearly predicted for birds close to the origin but I had low sample sizes for many of these species e.g. Yellow-bellied Sapsucker, Black-capped Chickadee, and American Robin. A similar explanation holds for some species that vary in position between years. Sample sizes were low for Golden-crowned Kinglet, Solitary Vireo, Canada Warbler, Magnolia Warbler, Bay-breasted Warbler, Common Yellowthroat and Dark-eyed Junco in one or both years. Both Canada Warbler and Chipping Sparrow shifted position between years although sample sizes were somewhat higher. These species were higher at clearcut edges in 1995 than in 1996 (only Canada Warbler was significant) and this may be due to a temporary crowding effect. Crowding could have obscured habitat relationships in 1995.

2.2.6 *Vegetation characteristics of aspen stands*

Vegetation structure did not change substantially between edge types (Table 2.6). Not only were aspen stands adjacent to recent clearcuts relatively similar to the interior, but older clearcut edges did not appear to change significantly. Of the 17 characteristics examined, only the density of conifer trees and the number of deciduous saplings differed significantly between treatments. There was a significantly higher density of conifer trees in aspen stands next to white spruce than in the interior of aspen stands or in stands adjacent to 15 y old clearcuts. Number of deciduous saplings were significantly higher in aspen stands adjacent to 15 y old clearcuts but not more so than in aspen next to recent clearcuts or in aspen next to white spruce. Both number of small snags and large CWD volume were marginally significant. Small snags were more than double in number at aspen/15 y old clearcut edges vs. aspen/white spruce edges. Volume of large CWD was 2-3 times lower at aspen/15 y old clearcut edges than at other edge types.

Mature and old stands had distinct vegetation structures (Table 2.7). Older stands had a higher density of deciduous canopy- and subcanopy-height trees, lower canopy cover, higher canopy height, fewer small snags and a higher large snag volume, more deciduous poles, higher % CWD cover and higher volume of large CWD.

I further analysed the difference in deciduous saplings between edges types to determine if deciduous saplings were significantly higher at the 15 y old clearcut edge than other edge types in both mature and old aspen stands. Analysis of variance using both age and edge type showed no interaction effect on deciduous saplings (ANOVA, F=0.59, p=0.628). Mature stands next to older clearcuts did have higher numbers of deciduous poles than older stands next to older clearcuts but this difference was not significant (Figure 2.9).

2.3 Discussion

2.3.1 *Lack of edge effect*

Contrary to many studies of forest edge, my research showed that songbird communities did not differ in density or species richness between edge types. However, when the variation due to vegetation was accounted for in the regression analysis, songbird densities were significantly higher at aspen/clearcut edges than the interior in 1995. In 1996, this difference between edge types disappeared. This suggests a crowding effect occurred at aspen/clearcut edges immediately post-harvest. Temporary increases in abundance immediately after fragmentation have been noted in boreal systems by Darveau (1995) and Schmiegelow *et al.* (1997) and in other systems by Whitcomb *et al.* (1981), Lovejoy *et al.* (1986) and Hagan *et al.* (1996). However, the crowding effect shown in this study was associated specifically with edge; total area of the aspen stand had no effect on songbird densities. Increased densities can result in lower pairing success (Hagan *et al.* 1996) but further study is necessary to determine if this occurs in the boreal forest.

The lack of an edge effect on songbird communities in the second year post-harvest can be attributed to the fact that vegetation structure was not substantially different between treatments. There are two explanations for the similarity of vegetation between my sites, both of which are linked to stand age. Firstly, in mature stands, surveys were probably conducted too soon after harvesting to allow sufficient time for the shrub layer to respond to increased light levels. Mature stands had a suppressed understorey because they had a closed canopy and little light reached the forest floor. Eventually, the understorey may develop in response to light at the edge (but see discussion below). Secondly, older stands had a dense understorey of alder (as seen in Table 2.7 where deciduous poles are 76% higher in old stands than mature stands). Here, the understorey layer was already well-developed in response to treefall gaps within the stand; therefore, understorey vegetation was unlikely to respond to increased light levels at the edge even if there was enough time for shrub layers to respond. Similarly, Noss (1991) showed that as gap heterogeneity (as measured by abundance of canopy gaps) within a stand increased,

the effect of edge decreased because birds were equally attracted to the dense shrubs at the gaps.

Many studies that have shown edge effects on songbirds were conducted in forests with either little understorey e.g. conifer stands in Scandinavia (Helle 1985) or high primary productivity e.g. tropical rainforest in Brazil (Lovejoy *et al.* 1986) or had range in these qualities e.g. climax hardwood stands in the U.S. (Garrison *et al.* 1977, examples in Lay 1938, Johnston 1947, Gates and Gysel 1978, Kroodsma 1984b). Over time, after an anthropogenic disturbance, these types of stands may be more likely to develop vegetation differences, and concurrent density differences in songbirds, between the edge and interior than older aspen stands. A low understorey may indicate a suppressed shrub layer that would develop in response to light. High productivity stands often already have a dense understorey but understorey layers probably receive more light at the edge than in the interior and develop further. Finally, most of the edges used in these studies were older than those used in my study and thus, had more time to for vegetation to respond to changes in light levels.

Neither migration, nesting nor foraging strategy of songbirds affected their response to forest edge. A number of studies show that many neotropical migrants are interior species that are sensitive to fragmentation (Whitcomb *et al.* 1981, Robbins *et al.* 1989, Rich *et al.* 1994). In contrast, Gates and Gysel (1978) and Gates and Giffen (1991) found neotropical migrants were attracted to edges. Neither circumstance applies here. Ground-nesting species can be more susceptible to the increased predation rates that often attends the creation of edge (Whitcomb *et al.* 1981). If edges are a source of predation and these species are adapted to the creation of edge in the boreal forest, they may avoid aspen/clearcut edges. Given other research that predicts that ground nest predation is low in this system (see Chapter 4), no selection pressure to avoid edges from this source may exist. Hansson (1983) found an increase in tree-gleaning species at conifer/clearcut edges that he attributes to higher numbers of available insects. In my study, availability of invertebrates may not be different between edge types or it may not be an important factor

influencing territoriality as neither foliage- nor ground-gleaning species had increased densities at the edge (see Chapter 3).

Vertical and horizontal heterogeneity within an aspen stand were more important predictors of songbird community composition and density than edge type, once crowding effects were no longer a factor. A similar relationship was shown by Schieck and Nietfeld (1995) for boreal birds as I have shown in this study: understorey complexity, stand age and canopy cover, and white spruce had a strong effect in models of songbird density and/or community pattern.

2.3.2 Natural vs. anthropogenic edges

Overall, songbird communities in the interior, at aspen/white spruce and aspen/clearcut edges were similar. Aspen/white spruce edges tended to be graded and there was some mixing of tree species on both sides of the edge while aspen/clearcut edges had a very narrow ecotone and high contrast. These qualities did not affect overall densities or species richness.

For a minority of species, edge type had an effect on density but the response was almost entirely to the aspen/white spruce edge. Western Tanager, Black-throated Green Warbler, Golden-crowned Kinglet and Dark-eyed Junco are associated with abundance of spruce and were likely attracted by the availability of habitat at this edge type. Birds that had low densities at aspen/white spruce, e.g. Red-eyed Vireo also tended to be negatively correlated with spruce abundance. There was little effect of aspen/clearcut edge at the species level: only Canada Warbler in 1995 showed an increase at aspen/clearcut edges and this effect did not carry through to 1996.

Aspen/clearcut edges acted as a boundary for many species in either year whereas aspen/white spruce edges did not. At aspen/clearcut edges, very little forest habitat was provided beyond the forest edge, therefore, species associated with forests were less likely to be detected across the edge. Also predation risk is often higher in an open area and this may restrict the movement of birds into the clearcuts (Desrochers and Hannon 1997). However, more species were consistently attracted to the aspen/clearcut edge than the

aspen/white spruce edge even though overall densities did not differ. Species may be using the clearcut edge for its songpost potential (Kroodsma 1984a). Some species may prefer to sing at the clearcut edge rather than within the forest because sound waves will travel further when there is no forest present to scatter or reflect them (Gerhardt 1983).

The aspen/clearcut edge was also a boundary for species that had significantly higher densities in clearcuts than in the adjacent forest. Species that were distinct to clearcuts are unlikely to act as a source of competition for forest species. Similarly, species found in aspen that also freely use the clearcuts e.g. Mourning Warbler, White-throated Sparrow and Chipping Sparrow, don't seem to gain any competitive advantage within the forest, as suggested by Ambuel and Temple (1983). Their densities in aspen next to clearcuts are no higher than those in the forest interior.

In summary, the graded edge was much more permeable (*sensu* Weins *et al.* 1985), with birds using habitat both sides of the edge, than the abrupt edge that acted as a boundary for bird settlement. Because I did not separately test the effects of edge contrast and ecotone width, I was unable to distinguish their individual effects on songbird response. In conjunction, edge contrast and ecotone width successfully predicted the tendency of an edge to act as a habitat boundary.

2.3.3 *"Edge" vs. "interior" species*

The boreal forest does not appear to have species that are distinct to the edge or the interior in contrast to what has been shown in other systems (Johnston 1947, Whitcomb *et al.* 1981, Robbins *et al.* 1989, de Casenave *et al.* 1997). However, birds may change their behaviour at a clearcut edge as opposed to continuous forest. At aspen/clearcut edges, Least Flycatchers, Red-eyed Vireos, Tennessee Warblers and American Redstarts were detected singing more often at the edge in both years but their densities at these sites are not any higher than in the interior of the forest. Unfortunately, it is not known whether this behaviour change conferred any advantage such as increased pairing success.

Although Elliot (1987) and Small and Hunter (1989) did not find an effect of edge on density at the community level, both studies documented species that were specific to edge

or interior habitat; therefore, the boreal forest seems unique in this respect. Hansson (1983), working in spruce/pine stands in the boreal forests in Sweden, notes a similar phenomenon as that seen in my study: species restricted to the "edge" or "interior" were not present. Edge species are often associated with the shrub or brush habitat that may develop at some forest edges (e.g. Johnston 1947, Anderson *et al.* 1977, Freemark and Merriam 1986, Morgan and Gates 1992). Since changes in vegetation between edge and interior were not present in my study area, I would not expect to see changes in the species assemblage.

Caution should be applied in utilising "edge" and "interior" classifications from one study to another (e.g. Freemark and Merriam 1986) because site choice may not be consistent between landscapes. For instance, Whitcomb *et al.* 1981 stated that Ovenbirds and American Redstarts were interior species and Chipping Sparrows and Least Flycatchers were edge species. Although Chipping Sparrows and Least Flycatchers used the clearcuts, none of these four species had a different density at the edge from the forest interior.

2.3.4 *Edge effects in the future?*

Although I did not survey birds in aspen stands adjacent to older clearcuts, measurements of vegetation provide some predictive power as to the likelihood of an edge effect developing as clearcuts regenerate. Vegetation explained from 27-60% of variation in songbird density. Vegetation in aspen stands next to 15 year old clearcuts was similar to my other treatments for most characteristics; therefore, there may be no edge effects on birds in the future. DeGraaf (1992) attributes the lack of a unique songbird community at the edges of regenerating clearcuts in his study to the extensive forest cover in the region and rapid regeneration of clearcuts. He notes that in an extensively forested landscape, "edge" species are not abundant and this limits their ability to colonise edges. In my study, open area species such as Lincoln's Sparrow and Clay-coloured Sparrow quickly (<1 y) established territories in new clearcuts; lack of a source population of "edge" species does not explain the similarity in species composition between the edge and interior of the

boreal forest. Other studies conducted in extensively forested regions have shown edge effects, e.g. Kroodsma (1984b). However, the rapid regeneration of aspen stands in the boreal forest may limit the development of vegetation at the edge by quickly limiting any increases in the amount of insolation reaching the edge. After clearcutting, aspen regenerates by suckering and a closed canopy is achieved in as little as 3-4 years (Peterson and Peterson 1992).

The difference in aspen stands adjacent to older clearcuts that is most likely to have an impact on songbird populations is the difference in deciduous saplings. Deciduous saplings doubled in number at aspen/15 y old clearcut edges from levels found in interior stands. As seen in the ordination analysis of community pattern, an increase in understorey could have an impact on species that were strongly affected by understorey differences (e.g. Ovenbird, American Redstart, Yellow Warbler). However, number of deciduous saplings was 1.6 times as high in aspen/clearcut sites than interior sites and no differences in densities of these species were found. A further increase to levels in aspen/older clearcut sites may not have a strong effect. Finally, although the difference in number of deciduous saplings between old and mature stands was not significantly different, in mature stands, number of saplings was 2.6 times higher in stands next to older clearcuts than in interior stands. Possibly, these stands may show some edge effects in the future.

2.4 Management implications and directions for future research

My research predicts that the creation of clearcut/aspen edges will not be a source of habitat loss in addition to the clearcut itself. Densities at clearcut edges, besides a possible crowding effect in the first year post cut, were not different compared with either the forest interior or a natural forest edge. Although this research used observations of territorial birds, my conclusions were based on density not breeding success. Data on reproductive success are critical for drawing clear conclusions about the impact of edge because density does not necessarily correlate with reproductive success (Van Horne 1983, Vickery *et al.* 1992, Hagan *et al.* 1996).

Community level results tend to reflect the trends shown by the most abundant species. Many species held too few territories within my grids for me to perform any meaningful analysis. Other species, such as Cape May Warbler and Yellow-bellied Flycatcher, were detected but I could not determine their territoriality with confidence. Some resident species such as woodpeckers, bred earlier in the year and their territories were not detected by my surveys. Extending survey periods into the earlier portion of the season would effectively cover resident species. Rare birds such as Blackburnian Warbler, Bay-breasted Warbler, and Magnolia Warbler require a more intensive effort that focuses specifically on their settlement patterns and breeding success at edges.

Maintaining the natural range of vertical and horizontal heterogeneity will be critical for maintaining songbird communities in the boreal forest during logging operations. Although there was variation between years and models, variables predicting songbird density and community pattern were consistently related to heterogeneity. This should be a higher priority than managing the amount of forest edge created during logging operations. The current range of mixing of white spruce and aspen within stands should be sustained. Clearly, variation in tree species composition will provide for a range of songbird communities. Operating guidelines for aspen harvest require the reforestation of harvested conifer (Alberta Environmental Protection 1993) but maintaining a similar mix of tree species as was found on site before harvest should also be considered during restocking efforts.

Shorter rotation lengths that remove the older stands from the landscape will remove habitat for many species and should be avoided. Based on stand ages from AVI data, stands aged 110 years or more should be maintained. Schieck and Neitfeld (1995) further recommend creating gaps in mature stands to simulate conditions caused by treefall gaps in old stands if longer rotations are not an option. I hesitate to endorse this because individual site conditions may not produce the shrub understorey similar to that in old growth aspen. At shorter rotation lengths, mature stands will eventually dominate the landscape as older stands are brought into rotation. Vegetation may change at the edge of mature stands over time and songbird communities may also be affected. I encourage

further study on songbird communities at older ($\geq$ 15 y) edges of aspen stands adjacent to clearcuts, especially mature stands, to determine if these edge types are a source of habitat loss for songbird species.

Table 2.1. Review of literature on edge effects on songbird communities in chronological order including location, edge type and major results. In most of these studies, response of songbird communities to an edge can be explained by the degree of diffeerence in vertical heterogeneity of vegetation at the edge vs. interior (but see Hansson *et al.* 1983). None of these studies examined recent (≤2 y) clearcut edges.

Edge effect detected

Study	Location	Edge type(s)	Results
Lay 1938	Texas	pine-oak-hickory/clearcut	increased abundance and richness
Johnston 1947	Illinois	oak-maple/farmland.road	increased abundance and richness
Laudenslayer & Balda 1976	Arizona	pinyon pine-juniper/ ponderosa pine	diversity lower in ecotone
Anderson *et al.* 1977	Tennessee	hardwood/ transmission line corridors	increased density and diversity at 30.5 m corridor but not 12 m vs. interior
Gates & Gysel 1978	Michigan	oak-hickory/field	increased abundance and richness at edge vs. interior
Strelke and Dickson 1980	Texas	pine-hardwood/clearcut	increased abundance, diversity, richness at edge vs. interior
Helle & Helle 1982	Krunnit Islands off Finland	deciduous forest/meadow	increased density but decreased richness and diversity vs. interior
Morgan & Gates 1982	Maryland	mixed deciduous forest/field and forest+hedgerow/field	higher richness, abundance, diversity at hedgrow+forest edge vs. open forest edge
Kroodsma 1984b	Tennessee	oak-hickory/powerline corridor	interior species decreased in density at the edge while edge species increased
Hansson 1983	Sweden	scotch pine-Norway spruce/clearcut	increased density at the edge vs. interior
Helle 1985	Finland	coniferous forest/clearcut	increased density but decreased richness at edge vs. interior
Lovejoy *et al.* 1986	Brazil	rainforest/clearcut	decreased densities at edges vs. interior; no change at treefall gaps in interior

--continued--

Study	Location	Edge type(s)	Results
Noss 1991	Florida	hammock/gaps, bayheads,old fields, powerlines	increased densities at edge vs. interior; effect increased as gap and bayhead abundance decreased (dilution effect)
Gates & Giffen 1991	Appalachian mountains (Maryland)	deciduous/coniferous/ rhododenron shrub at stream bank	increased richness, density and diversity in NTM's as increase veg complexity to max at stream edge
DeGraaf 1992	New Hampshire	abrupt: seedling/sawlog, sapling/lg sawlog intermed: seedling/pole, sapling/sawlog,pole/lg.sawlog subtle: pole/sawlog,sawlog/lg. sawlog	highest avoidance of edge when stands most different similarity of spp. composition increases as ht./age contrast decreases
Cieslak 1992	Poland	pine/agricultural field	increased density and richness at edge vs. interior
Rich *et al.* 1994	New Jersey	oak-pine or hardwood swamp/ 8, 16, 23 m corridors	decrease in interior NTM's at wider corridors increase in abundance at 8 m vs. interior
de Casenave *et al.* 1998	Argentina	forest/grassland	abundance and species richness higher at edge vs. interior

No edge effect detected

Study	Location	Edge type(s)	Results
Elliott 1987	Maine	hardwood/clearcut mixedwood/clearcut softwood/clearcut	no consistent effect of edge
Small & Hunter 1989	Maine	mixedwood/river mixedwood/ powerline	no consistent increase in density at the edge type

Table 2.2. Probability values and power at α=0.10 from 2-way ANOVAs analysing the effect of edge type and year on songbird guilds. See Appendix 2.3 for list of species classified by guild.

Guild	Edge type		Year		Edge type * Year	
	p	1-β	p	1-β	p	1-β
Neotropical migrants	0.145	0.53	0.154	0.41	0.527	0.42
Short distance migrants	0.167	0.50	0.011	0.84	0.922	0.12
Shrub nesters	0.400	0.31	0.027	0.73	0.519	0.25
Ground nesters	0.365	0.32	0.633	0.21	0.600	0.22
Foliage gleaners	0.329	0.35	0.32	0.26	0.717	0.18
Ground gleaners	0.714	0.18	0.001	0.96	0.474	0.27

Table 2.3. Results of Kolmogorov-Smirnov goodness-of-fit tests of observed and expected distributions of total detections of territorial species at aspen/clearcut and aspen/white spruce edges. Only species for which there were at least 15 detections in total are included.

		1995			1996	
Aspen/Clearcut Edge	n[†]	p	E/I[‡]	n	p	E/I
Least Flycatcher	74.5	0.005<p<0.01	E	57	<0.001	E
Red-breasted Nuthatch	0	n/a		17	NS	
Warbling Vireo	15	0.005<p<0.01	E	8	n/a	
Red-eyed Vireo	78	<0.001	E	74.5	<0.001	E
Tennessee Warbler	36	<0.001	E	130.5	<0.001	E
Yellow Warbler	26	NS		20	0.05	E
Yellow-rumped Warbler	16	0.005<p<0.01	E	27	NS	
American Redstart	37	0.05<p<0.10	E	25	0.002<p<0.005	E
Ovenbird	54.5	<0.001	E	41	NS	
Mourning Warbler	38.5	0.05<p<0.10	I	26	0.05	E
Rose-breasted Grosbeak	22	0.001<p<0.002	E	11	n/a	
White-throated Sparrow	72.5	NS		73	<0.001	E
Aspen/White spruce						
Red-breasted Nuthatch	7.5	n/a		46.5	<0.001	E
Red-eyed vireo	8	n/a		22	NS	
Tennessee Warbler	31.5	NS		99	NS	
Yellow-rumped Warbler	19	NS		39.5	0.02<p<0.05	E
Black-throated Green Warbler	38	NS		32	NS	
Ovenbird	46	NS		32	NS	
Connecticut Warbler	10	n/a		27	0.002<p<0.005	E
Mourning Warbler	26	NS		28	NS	
White-throated Sparrow	42.5	0.001	I	63	<0.001	E
Western Tanager	18.5	NS		21	NS	

†Total number of detections in all grids in treatment.
‡Indicates whether detections are highest at the edge (E) or interior (I).

Table 2.4. Stepwise multiple regression models of effects of edge type, stand age, stand heterogeneity and vegetation characteristics on songbird territory density (*see text for further explanation*).

Year	Final model	adjusted R^2	F	p
1995	1.35 + 0.18(Aspen/Clearcut Edge) - 0.012(Canopy Cover)	0.60	13.092	0.0006
1996	0.77 + 2.19(Gap Heterogeneity) + 0.12(Deciduous Poles) - 0.006(Canopy Cover)	0.42	6.276	0.0038

Table 2.5. Canonical coefficients and inter-set correlations for vegetation variables used in redundancy analysis. Results are reported for the first 2 axes only. * indicates significance based on t-values at p≤0.10.

Year	Variable	Canonical coefficients		Inter-set correlations	
		Axis 1	Axis 2	Axis 1	Axis 2
1995	Stand age	0.1934	-0.5505*	0.6221	0.3619
	Basal area of conifer trees	-0.4150*	1.1147*	-0.3432	0.7366
	Canopy cover	-0.7101*	-0.5424*	-0.8213	-0.3096
	Deciduous poles	0.0995	0.4693*	0.5958	0.1591
1996	Stand age	0.3577*	0.6590*	0.5885	0.5934
	Basal area of conifer trees	-0.4514*	0.6357*	-0.3445	0.7549
	Canopy cover	-0.4394*	-0.0063	-0.5888	-0.3297
	Deciduous poles	0.3420*	-0.2467	0.6993	-0.0480

Table 2.6. Comparison of vegetation characteristics in 0.04 ha plots in the interior of aspen stands to aspen/recent clearcut, aspen/15 y clearcut and aspen/white spruce edges monitored in 1996.

Variable	Interior	Aspen/ Clearcut	Aspen/ 15 y old Clearcut	Aspen/ White spruce	F	p
Basal area of trees (m²):						
Deciduous Trees	0.8303	0.8146	0.7806	0.8123	0.157	0.924
Subcanopy Trees	0.0087	0.0162	0.0175	0.0235	0.522	0.670
Conifer Trees	0.0501a†	0.0523ab	0.0309a	0.1334b	3.932	**0.019**
Canopy Cover (%)	60.6	59.8	55.5	60.1	0.568	0.641
Canopy Height (m)	24.8	25.3	24.4	26.6	1.054	0.384
Snags < 12 cm DBH (#)	10.3	13.1	20.2	8.0	2.249	0.104
Large Snag Volume (m³)	1.92	1.68	1.62	1.40	0.256	0.856
Deciduous Saplings (#)	20.8a	34.3ab	41.4b	25.3ab	2.390	**0.091**
Deciduous Poles (#)	5.4	5.3	6.2	3.2	0.447	0.721
Coniferous Saplings (#)	1.1	0.5	1.5	1.5	1.759	0.178
Coniferous Poles (#)	0.8	0.2	0.2	0.5	1.934	0.147
Shrub Density (/m²)	8.1	6.5	5.3	5.0	1.521	0.231
Green Ground Cover (%)	74.5	71.2	75.9	76.7	1.681	0.194
Shrub Cover (%)	36.6	32.8	36.5	40.6	0.865	0.471
Forb Cover (%)	28.3	25.6	31.7	27.4	1.056	0.384
CWD Cover (%)	5.0	6.7	5.8	5.8	0.886	0.461
DWD < 12 cm (#)	103.0	138.4	119.1	106.7	1.132	0.353
DWD > 12 cm (m³)	1.25	1.71	0.44	1.67	2.221	0.108

†A difference of one letter indicates significance of p<0.10.

Table 2.7. Comparison of vegetation characteristics of 0.04 ha plots in mature and old aspen stands monitored in 1996. Average age of origin for mature stands=1920 and for old stands=1870 based on Phase III and Alberta Vegetation Inventory maps.

Variable	Mature Aspen	Old Aspen	F	p
Basal area of trees (m^2):				
Deciduous Trees	0.8961	0.7539	6.376	**0.019**
Subcanopy Trees	0.0082	0.0228	4.963	**0.036**
Conifer Trees	0.0606	0.0938	1.194	0.286
Canopy Cover (%)	65.7	55.5	9.08	**0.006**
Canopy Height (m)	23.9	27.0	10.99	**0.003**
Snags < 12 cm DBH (#)	16.4	5.5	13.91	**0.003**
Large Snag Volume (m^3)	0.90	2.32	13.11	**0.002**
Deciduous Saplings (#)	26.3	27.3	0.028	0.870
Deciduous Poles (#)	1.7	7.1	9.59	**0.005**
Coniferous Saplings (#)	1.0	1.1	0.034	0.856
Coniferous Poles (#)	0.7	0.3	1.702	0.206
Shrub Density (/m^2)	7.1	6.1	0.440	0.514
Green Ground Cover (%)	74.6	73.7	0.128	0.724
Shrub Cover (%)	38.9	34.8	0.878	0.356
Forb Cover (%)	28.6	25.8	1.003	0.327
CWD Cover (%)	5.1	6.5	3.310	**0.082**
DWD < 12 cm (#)	115.6	116.4	0.0020	0.965
CWD > 12 cm (m^3)	0.62	2.32	20.57	**0.0002**
Spruce heterogeneity (Edge:area/grid area)	0.0672	0.0755	1.280	0.271
Gap heterogeneity (Edge:area/grid area)	0.540	0.0672	0.490	0.492

Figure 2.1. Location of the study area (Calling Lake) and extent of boreal mixed-wood forest in Alberta.

★ Calling Lake

Edmonton

Calgary

Boreal mixed-wood forest
Urban centres
★ Study Area
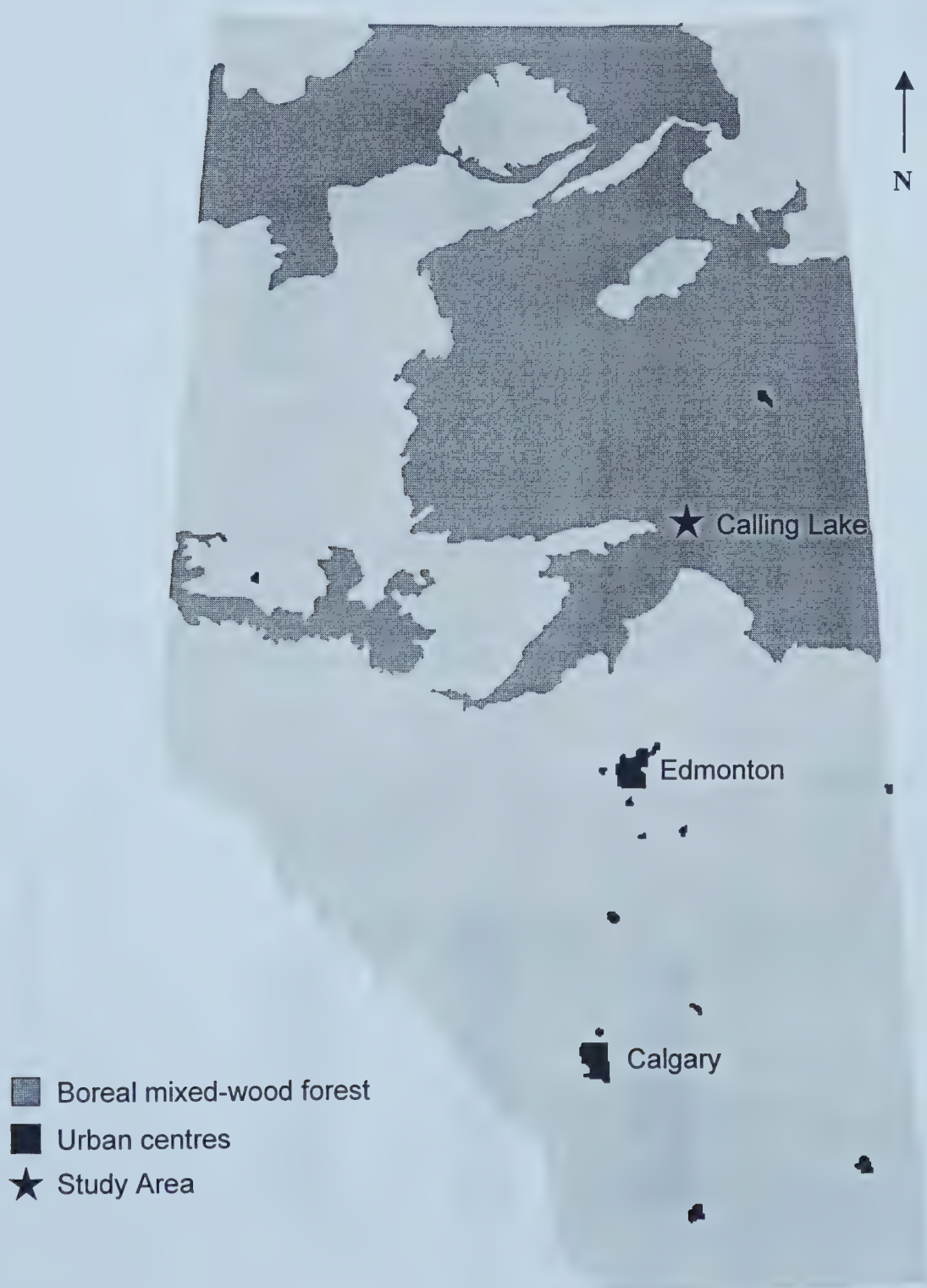
Figure 2.2. Territory density of songbird communities by edge type for 1995 and 1996 based on spotmapping surveys. Means reported ± SE.
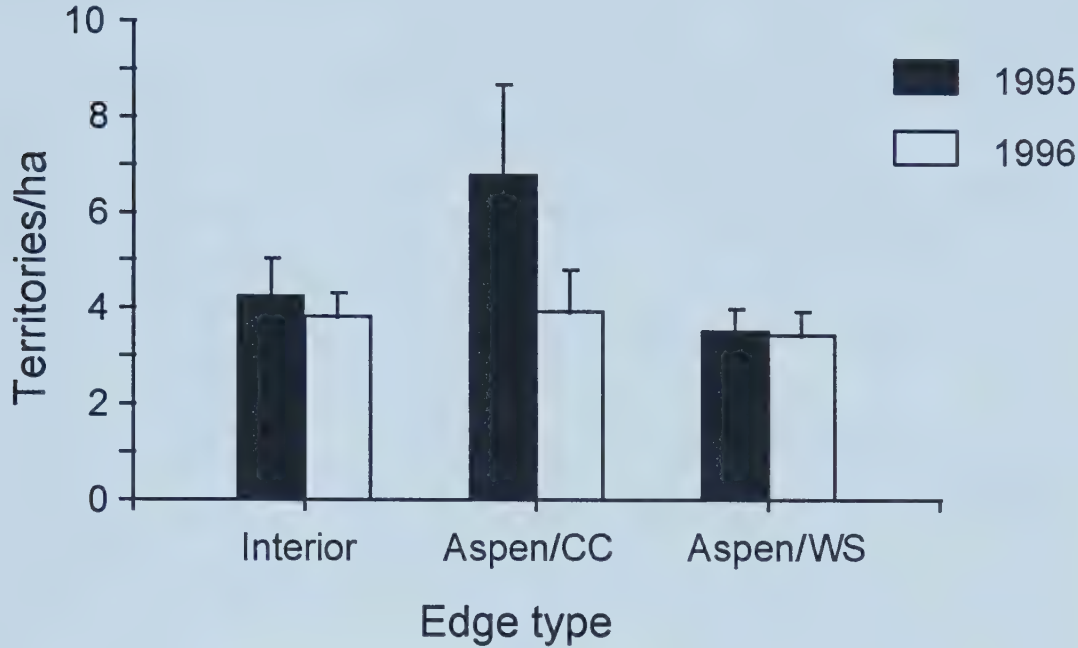
Figure 2.3. Species richness of songbird communties by edge type for 1995 and 1996 based on spotmapping surveys. Means reported ± SE.

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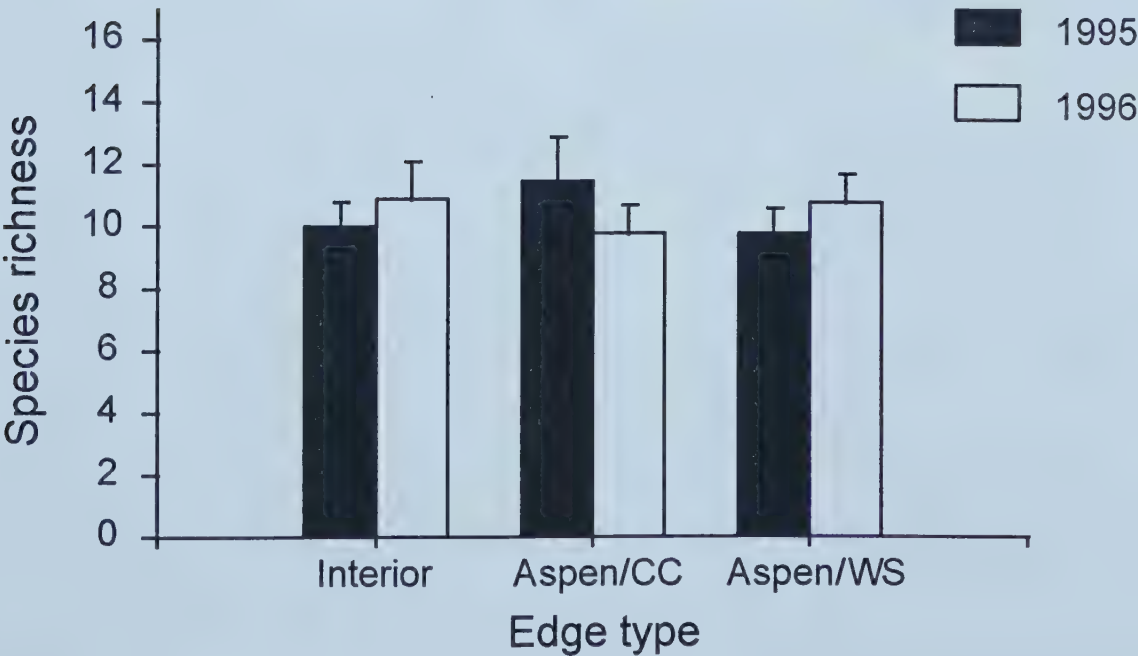
Figure 2.4. Dendrogram of songbird communities by edge type as produced from a cluster analysis. Communities do not cluster out by edge type. Clusters tend to be defined by structural characteristics of the stand as noted on the figure.

a) YEAR = 1995
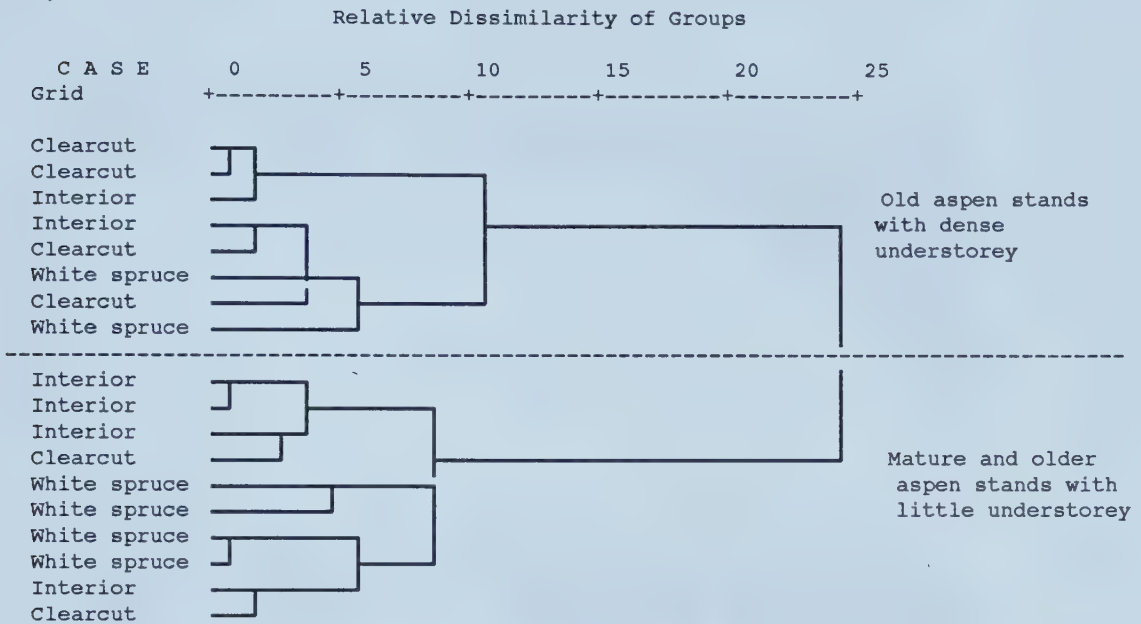
b) YEAR = 1996
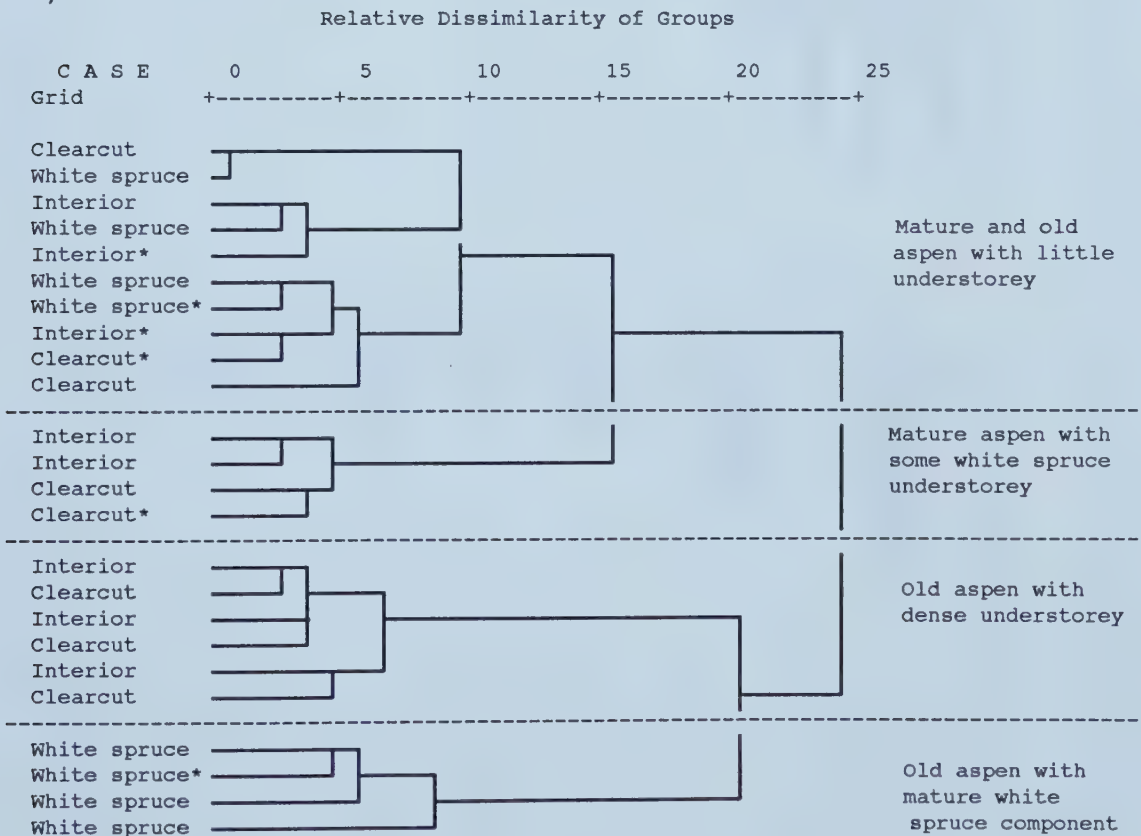
* = sites added in 1996

Figure 2.5. Bar graphs comparing mean territory density/ha of songbirds composing the communities at the interior of aspen stands in (a) 1995 and (b) 1996, aspen stand adjacent to clearcuts in (b) 1995 and (e) 1996, and aspen stands adjacent to white spruce in (c) 1995 and (f) 1996. Difference of one letter indicates significance at p<0.10 between edge types. n/a=not analysed due to small samples sizes (<1 territory). See Appendix 2.3 for long form of AOU species codes.

Figure 2.5. continued.

d) Interior 1996

e) Aspen/Clearcut 1996

f) Aspen/White spruce 1996
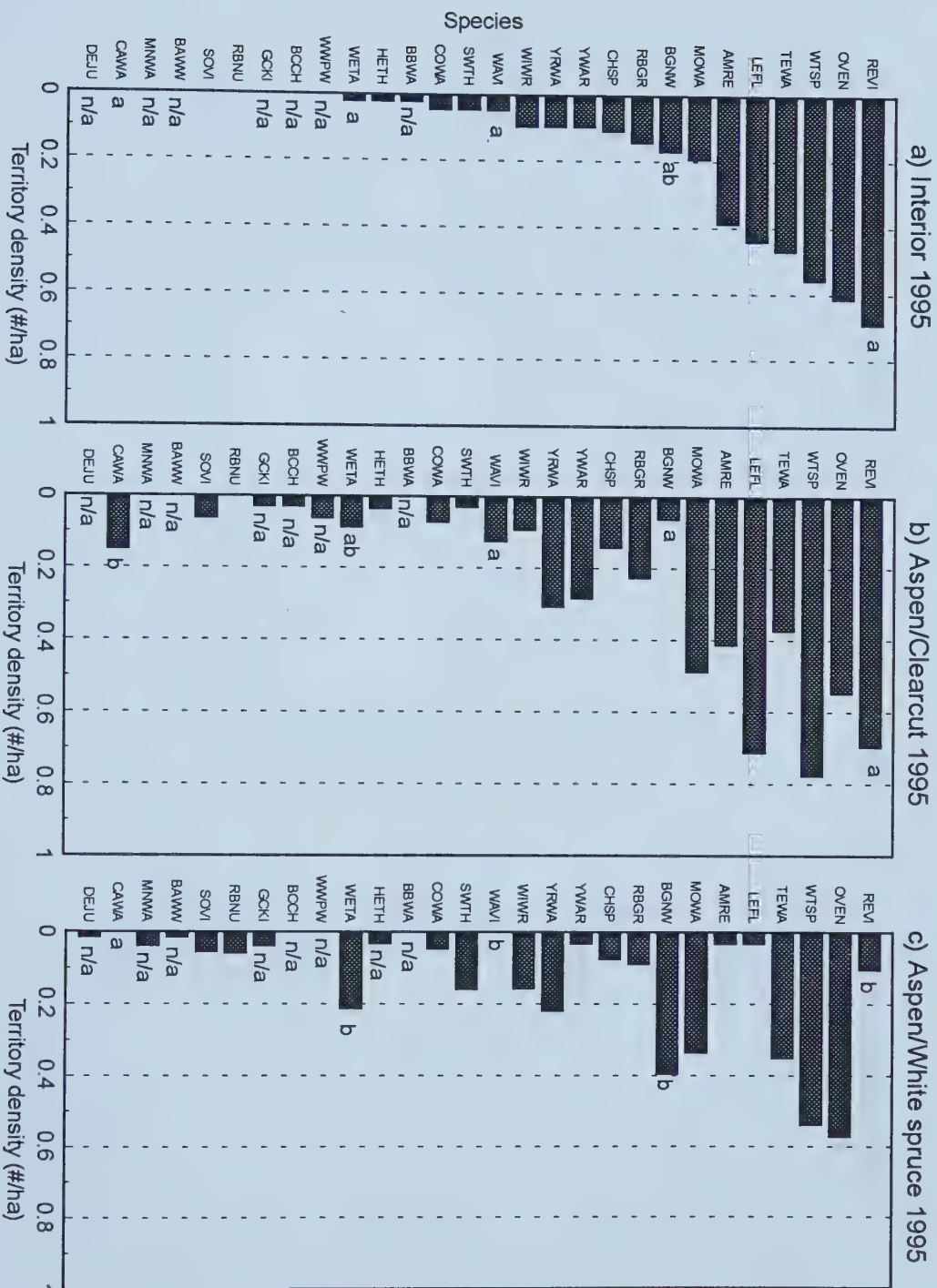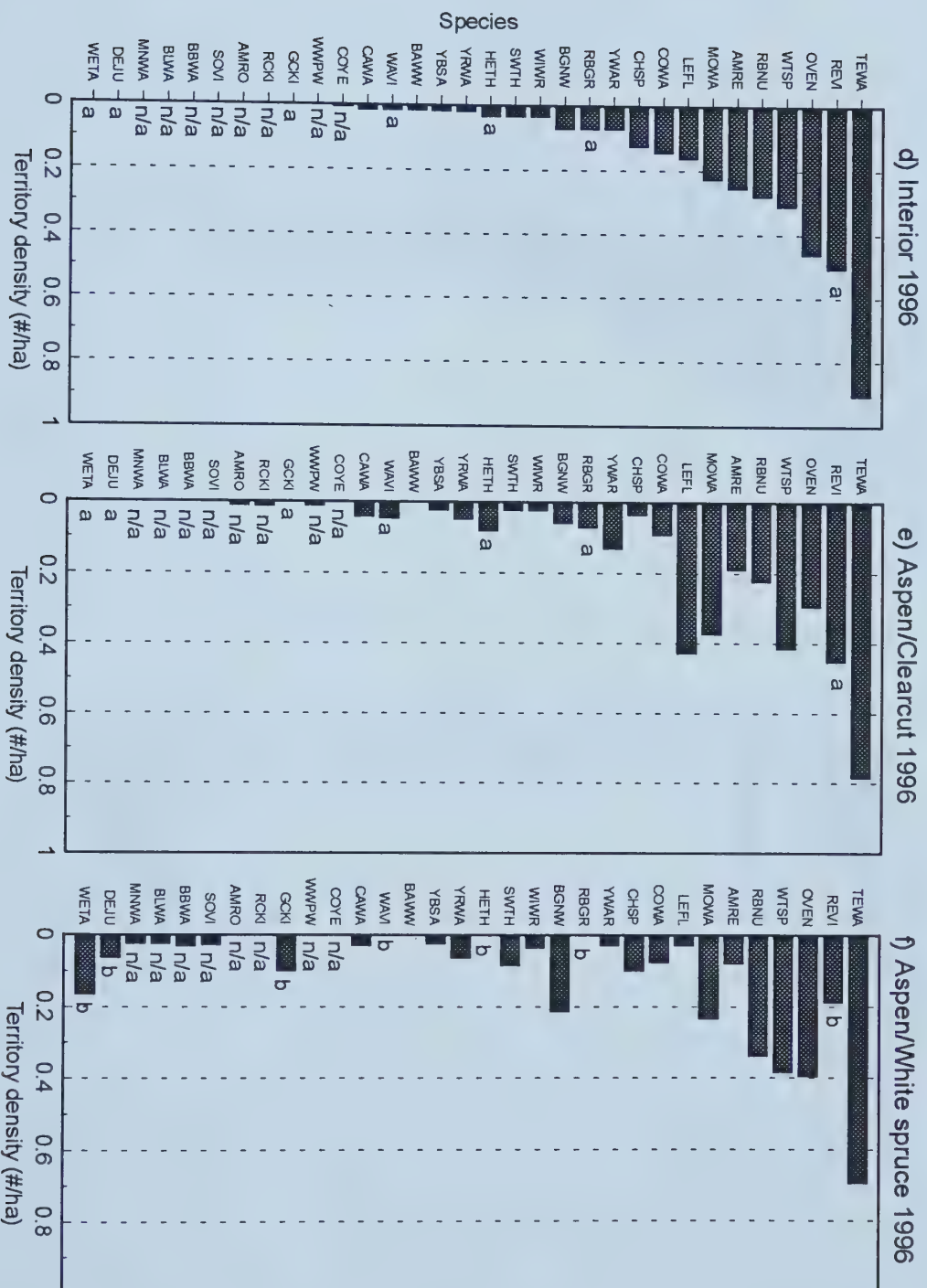
Figure 2.6. Bar graphs comparing mean territory density of songbird species in aspen stands and in adjacent clearcuts. Graphs represent aspen stands adjacent to clearcuts in (a) 1995 and (b) 1996 and clearcuts in (c) 1995 and (d) 1996. Difference of one letter indicates significance at p<0.10 between sites. n/a=not analysed due to small samples sizes (<1 territory). See Appendix 2.3 and 2.4 for long form of AOU species codes.
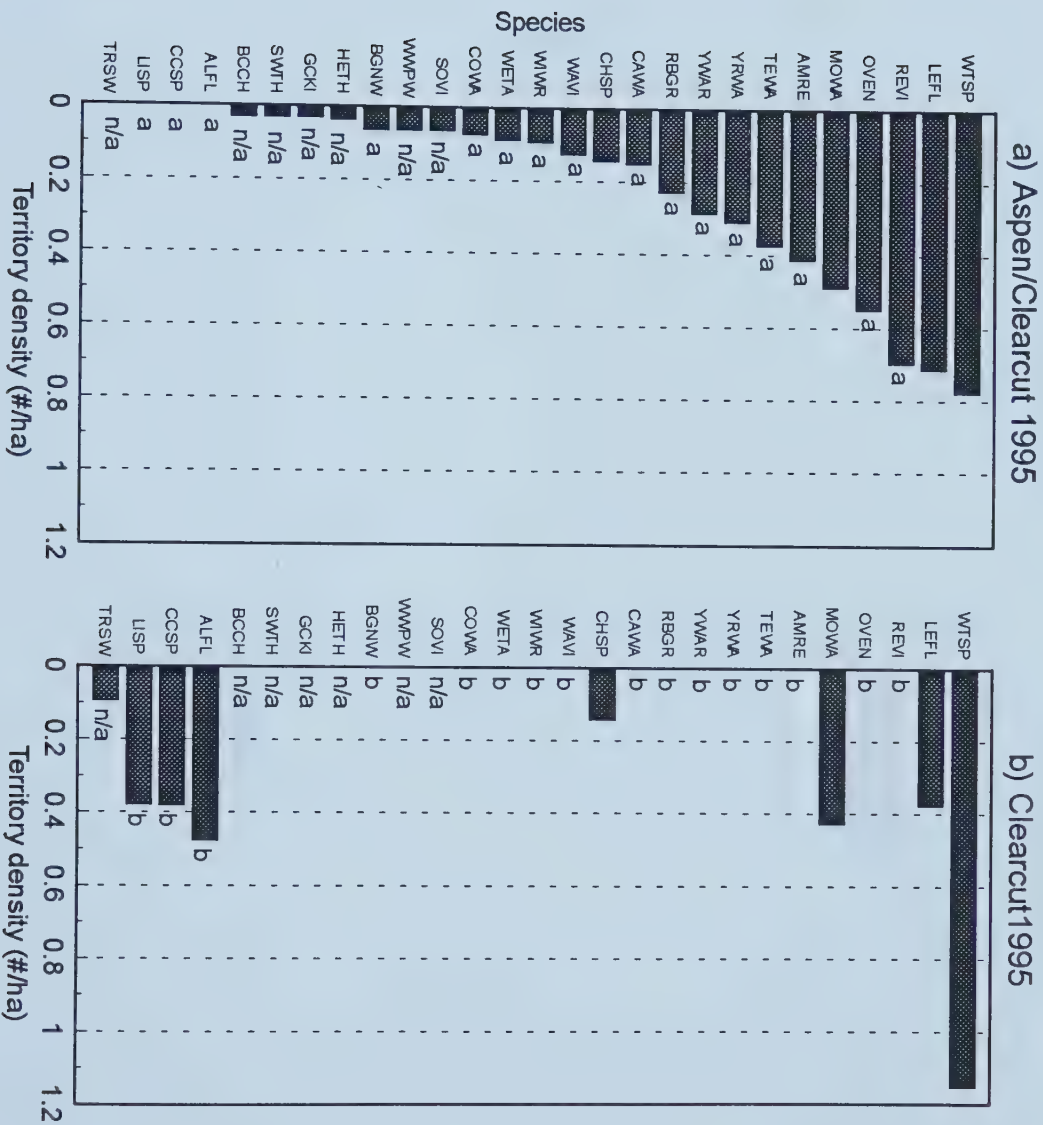
Figure 2.6. continued.
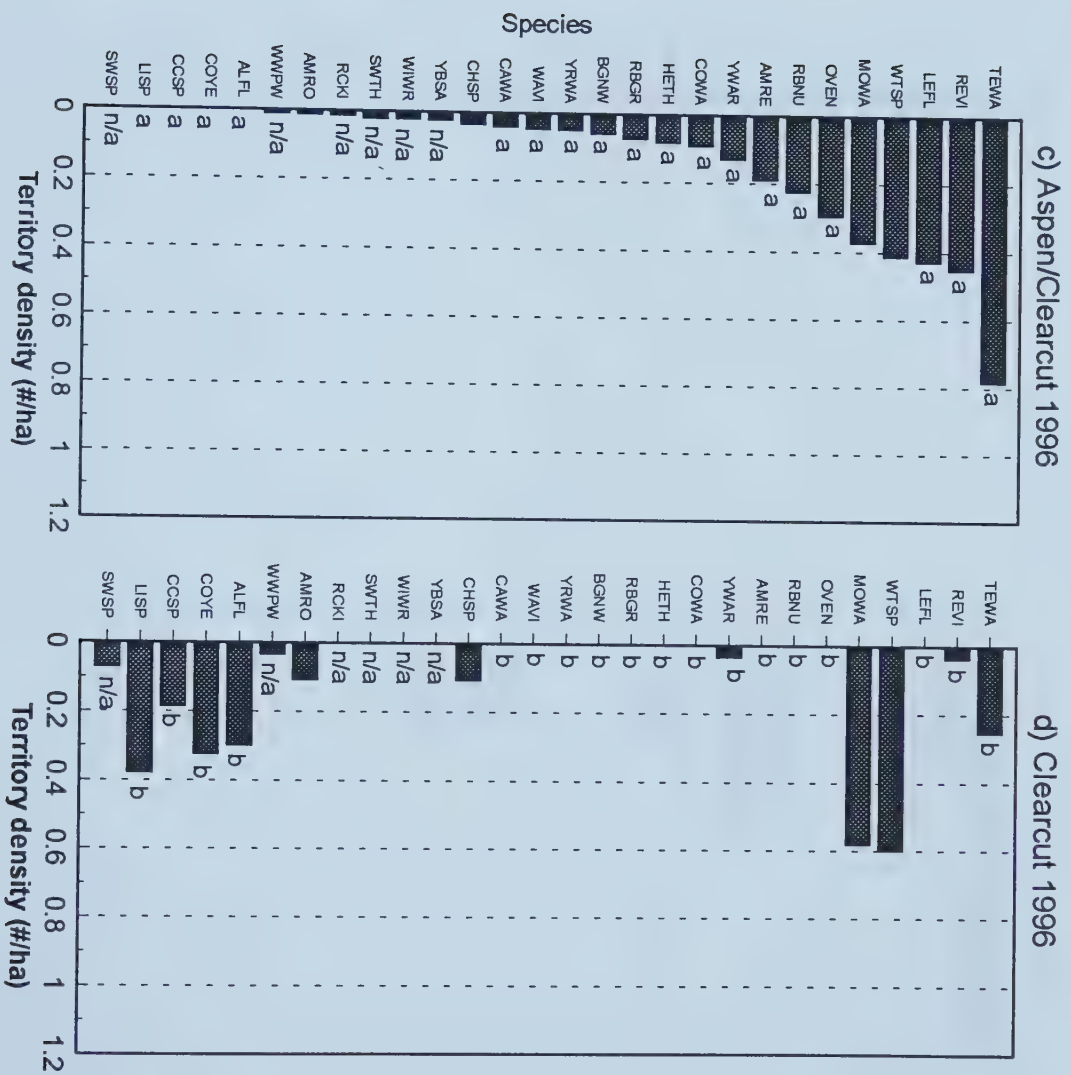
Figure 2.7. Bar graphs comparing mean territory density of songbird species in aspen stands and in adjacent white spruce. Graphs represent aspen stands adjacent to white spruce stands in (a) 1995 and (b) 1996 and white spruce stands in (c) 1995 and (d) 1996. Difference of one letter indicates significance at p<0.10 between sites. n/a=not analysed due to small samples sizes (<1 territory). See Appendix 2.3 for long form of AOU species codes.

a) Aspen/White spruce 1995

b) White spruce1995

Figure 2.7. continued.

c) Aspen/White spruce 1996

d) White spruce 1996
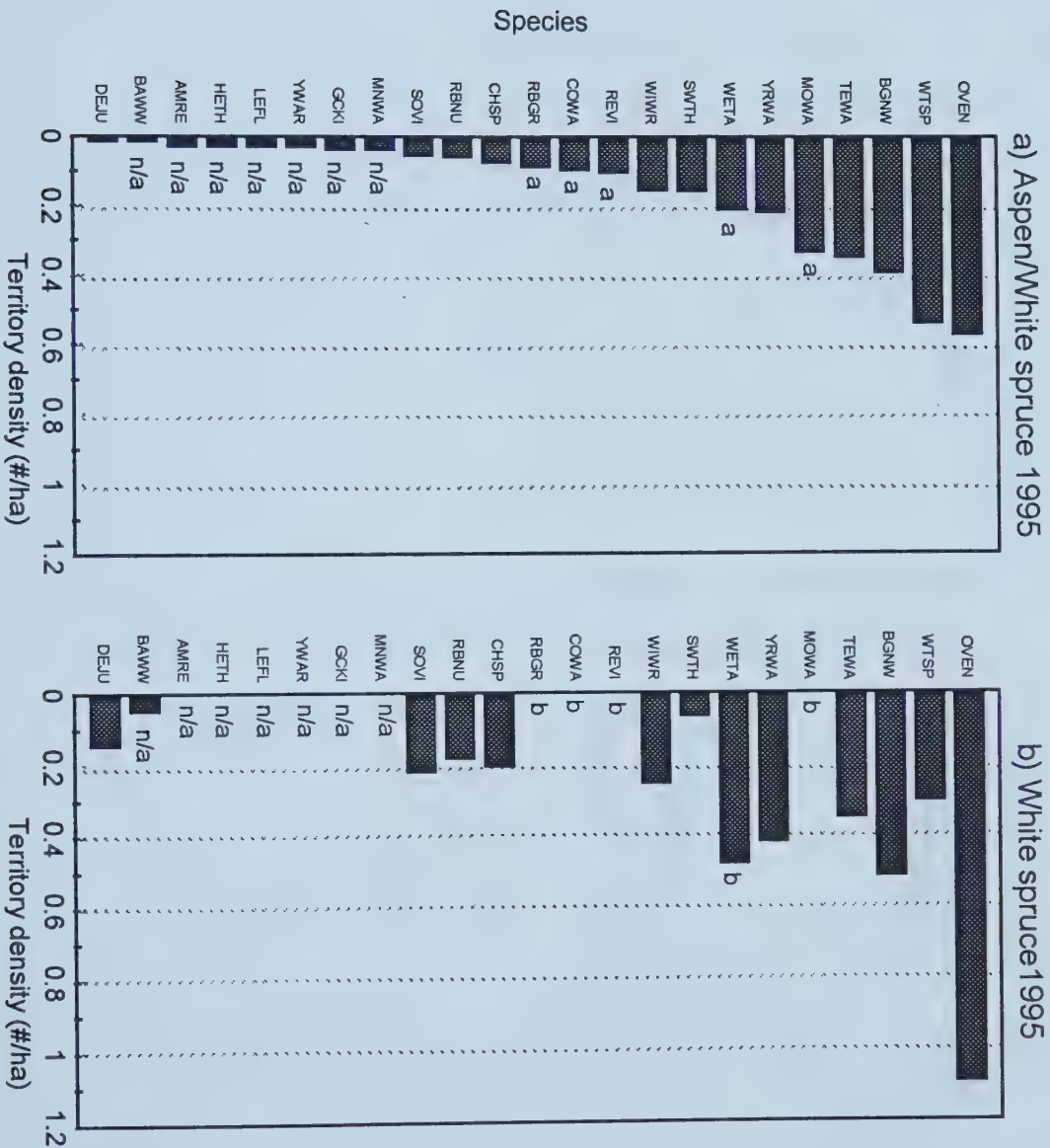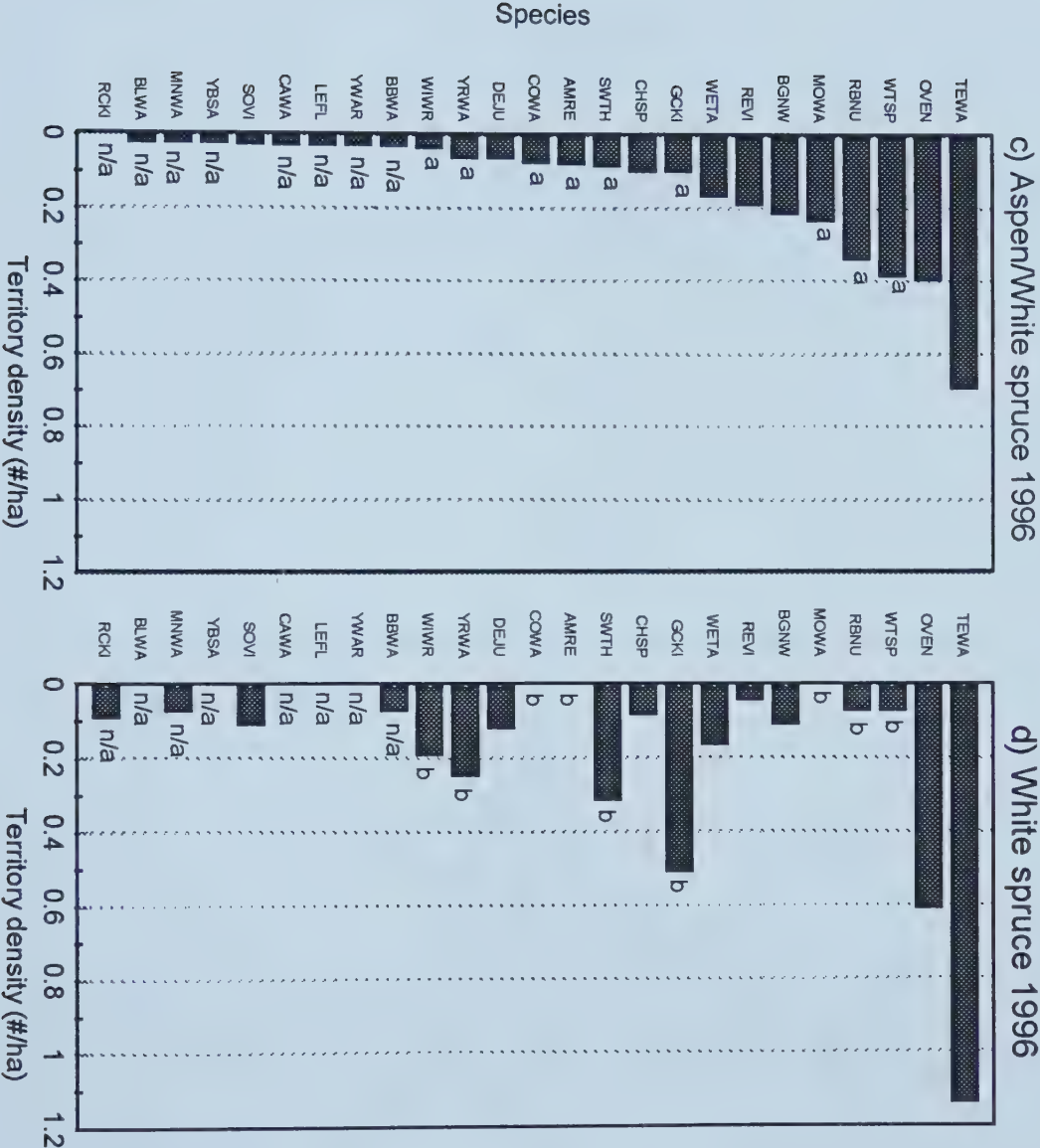
Figure 2.8. Biplots from redundancy analysis ordination of songbird territory density and vegetation characteristics of spotmapping grids in (a) 1995 and (b) 1996. See Appendix 2.3 for species codes.
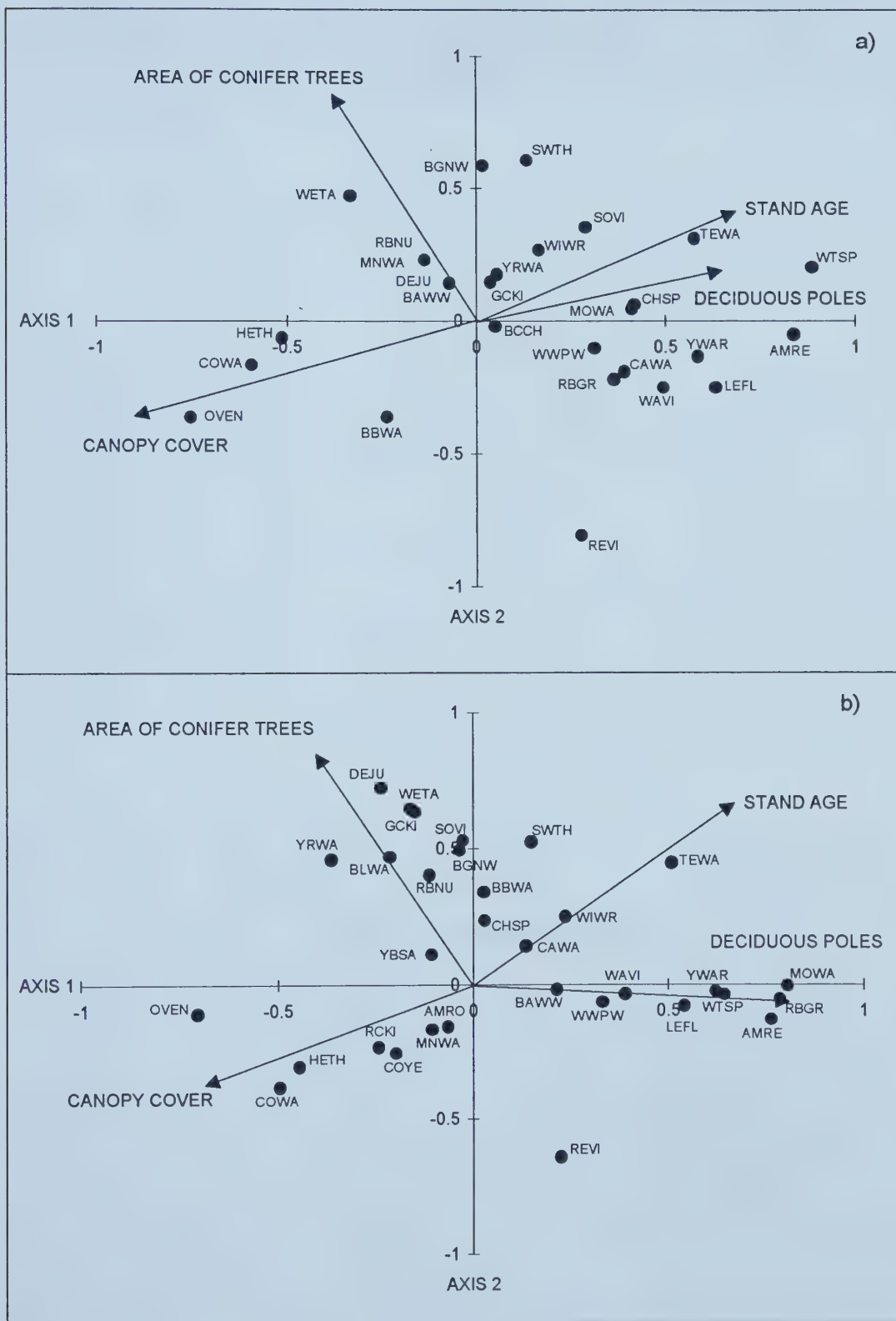
Figure 2.9. Mean (+/- standard error) number of deciduous saplings per plot (0.008 ha) in mature and old stands by edge type. Sapling number in aspen stands adjacent to older clearcuts was significantly higher than numbers in interior sites but more so in mature stands. Difference between stand ages was not statistically significant.
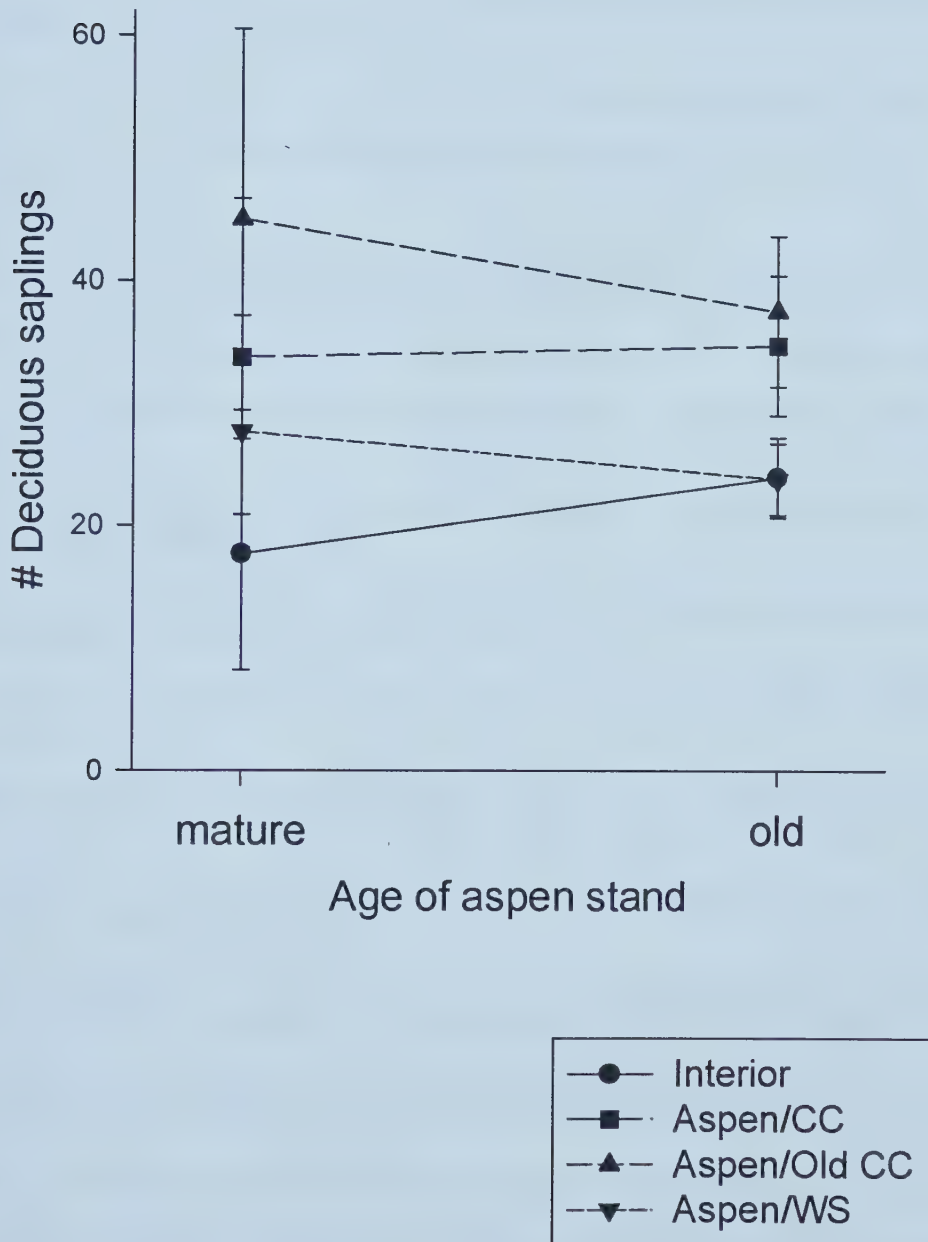
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Chapter 3: Invertebrate abundance at forest edges: consequences for boreal songbirds.

3.0 Introduction

Higher densities of songbirds are often observed at the forest edge, compared with the forest interior (Lay 1938, Anderson *et al.* 1977, Gates and Gysel 1978, Strelke and Dickson 1980, Hansson 1983, Helle 1985, Cieslak 1992 but see Elliott 1987). Increased numbers of songbirds may establish territories at the edge because availability of food is higher than in the interior, but this link is not well-established. Songbirds tend to settle at higher densities at the edge when there is higher structural complexity of vegetation there than at the interior, and where, some authors have suggested, food resources in the form of invertebrate abundance are also higher (Johnston 1947, Gates and Gysel 1978, Lovejoy *et al.* 1986, Noss 1991). Other studies have proposed that increased songbird densities at the edge vs. interior can be entirely attributed to increases in invertebrate availability found there (Hansson 1983). There are few empirical studies that test (1) whether overall abundance of invertebrates available to birds increases at forest edges relative to the forest interior (e.g. Helle and Muona 1983 in part), and (2) whether songbird response to edge is mediated by invertebrate abundance.

Research relating songbirds and invertebrate food supply is seemingly contradictory. Stenger (1958) and Burke and Nol (1998) found positive relationships between territory size and presence of Ovenbirds (*Seiurus aurocapillus*), respectively, and invertebrate abundance. Cody and Cody's (1972) research on wrens showed an inverse relationship with density and food supply. Nilsson (1979) suggested that invertebrate availability was the major determinant of songbird densities in forests of southern Sweden. However, Zach and Falls (1979) showed no correlation between Ovenbird territory size and food supply and, similarly, Blancher and Robertson (1987) showed no relationship between kingbird density and invertebrate abundance. If food supply is inversely related to territory size, songbird density should be directly related to invertebrate abundance (Newton 1980). However, this relationship may only hold within a range of densities: at high densities, numbers may be

limited by territoriality and at low densities, by intruder pressure (Newton 1980). Further, food may not limit densities if foraging occurs off territory (e.g. Zach and Falls 1979), if qualities relating to nest sites or mates are more important (Newton 1980), or if food is superabundant (Martin 1987).

Studies of individual insect species and orders suggest that many invertebrates are more abundant at the forest edge than the forest interior, specifically forest edges formed by clearings (Helle and Muona 1983, Fowler *et al.* 1993, Buse and Good 1993). The forest adjacent to a clearing can receive increased insolation and a concomitant increase in ambient temperature and decrease in humidity compared to the forest interior (Matlack 1993). Many species oviposit more frequently at the edge than the interior (Bellinger *et al.* 1989, Courtney and Courtney 1992) and warmer temperatures may result in shorter development times (Stamp 1990, Cappuccino and Root 1992). Conversely, high temperatures and low humidity at the edge can cause desiccation and death in some insects (Klein 1989, Ozanne *et al.* 1997). Vegetation at the forest edge adjacent to a clearing is often more abundant than in the interior, especially in the understorey (Ranney *et al.* 1981, Fraver 1994, Malcolm 1994), therefore availability of food can increase for phytophagous insects if vegetation has had time to respond to increased light levels at the edge relative to the interior. As has been shown for songbirds (MacArthur and MacArthur 1961, Willson 1974, Freemark and Merriam 1986), insect diversity can increase with increased vertical heterogeneity (or foliage height diversity) and species diversity of vegetation (Murdoch *et al.* 1972, Southwood *et al.* 1979, Lawton 1983, Buse and Good 1993). Quality of food for phytophagous invertebrates may increase at the edge vs. the interior as photosynthetic rates will increase in response to increased insolation (Maiorana 1981, Collinge and Louda 1989). Further, habitat fragmentation can facilitate population increases of phytophagous species by limiting the efficacy of their parasites and predators (Roland and Taylor 1995, Roland *et al.* 1997). Ultimately, response by invertebrates to forest edges can vary between species, seasons and habitats (Shreeve 1986, Didham 1997). Some species are attracted to the edge and the lighter, warmer conditions found there while others may avoid it and seek shadier, cooler

locations in the forest interior (e.g. Weseloh 1976, Rauscher 1979, Lovejoy *et al*. 1986, Bultman and Faeth 1988, Didham 1997).

The boreal mixed-wood forest of Alberta is a heterogeneous landscape due to variation in topography and a history of fire and insect outbreaks (Bonan and Schugart 1989, Peterson and Peterson 1992). Natural edges between patches of aspen (*Populus tremuloides*), spruce (*Picea glauca* and *P. nigra*), wetlands and water bodies are abundant here. Superimposed over this landscape are edges caused by anthropogenic activity. In the last 10 years, extraction of timber resources has increased dramatically across the landscape as changes to technology and governmental policy have permitted the harvest of aspen for the pulp and paper production (Pratt and Urquhart 1994). Clearcutting is conducted in a checkerboard fashion leaving alternating cut and uncut forest blocks and an extensive amount of forest/clearcut edge. Little is known about how invertebrates respond to either natural or anthropogenic edges in this system. Many invertebrates within Canada's boreal forest have yet to be identified and knowledge about species and their ecological relationships with other systems (such as avian systems) is mainly limited to species of economic importance (e.g. Sanders *et al*. 1985, Danks and Foottit 1989, Spence *et al*. 1997).

Research in this thesis (Chapter 2) showed that there were no differences in songbird densities at the community level between aspen/clearcut edge, aspen/white spruce edge and interior of aspen stands in the boreal forest, other than effects attributed to crowding at aspen/clearcut edges in the first year post-harvest. However, some differences in density at the edge from the interior were observed at the species level. Invertebrate abundance may explain some differences in songbird densities between edge types in the boreal forest. Because invertebrates are more sensitive to microclimate and vegetation quality than birds, and can respond rapidly to changes in these qualities, a difference between edge and interior may be expected. Aspen/clearcut edges may be brighter and hotter than the forest interior from increased insolation, although the abundance of canopy gaps within the forest interior may negate any difference. Aspen/white spruce edges may be darker and cooler than

aspen/clearcut edges and the forest interior and this may affect invertebrate abundance (Gullan and Cranston 1994).

In this study, I examined invertebrate abundance at a natural edge (aspen/white spruce), an anthropogenic edge (aspen/clearcut) and in the forest interior. I then determined whether songbird density was predicted by invertebrate abundance. Finally, I tested whether invertebrate abundance could be predicted by vegetation characteristics, as suggested by researchers studying songbirds at edges as well as entomological research. Although many species seem to prey opportunistically on available invertebrates, some studies have shown that birds have preferences for certain types of invertebrates (Stenger 1958, Cody and Cody 1972, Busby and Sealey 1982, Robinson and Holmes 1982, Guinan and Sealey 1987). Therefore, abundance was estimated using biomass for the entire community and for major groups of invertebrates. I measured biomass rather than numbers because small and large animals are not nutritionally equivalent as food sources for birds. Other than biomass, I did not measure other factors that influence availability e.g. how plant species and foliage structure affect the ability of birds to find invertebrates, how birds discover and capture invertebrate prey or diet preferences specific to boreal bird species (Holmes and Schultz 1988, Wolda 1990). However, if these other factors are relatively constant among edges, then invertebrate biomass should be a good relative measure of food availability among different sites. The majority of territorial bird species in my study area are either foliage or ground gleaning species (82%), 68% are foliage gleaners and 32% are ground gleaners (Chapter 2); therefore, I sampled foliage and ground dwelling invertebrates.

3.1 Methods

3.1.1 *Study area*

The study was conducted over 2 years (1995-96) in north-central Alberta, Canada, near Calling Lake (UTM Zone 12: 344214 E, 6133569 N) in boreal mixed-wood forest. Forested areas are dominated by stands of trembling aspen, *Populus tremuloides,* balsam poplar, *Populus balsamifera*, and white spruce, *Picea glauca*, on upland sites (Strong 1992).

Wetter sites are characterised by stands of black spruce, *Picea mariana* and willow, *Salix* spp. Major understorey species in aspen stands include: green alder, *Alnus crispa*, low-bush cranberry, *Viburnum edule*, prickly rose, *Rosa acicularis*, beaked hazelnut, *Corylus cornuta*, bracted honeysuckle, *Lonicera invulcrata*, and willow, *Salix* spp. Wild sarsaparilla, *Aralia nudicaulis*, dewberry, *Rubus pubescens*, fireweed, *Epilobium angustifolium*, bunchberry, *Cornus canadensis*, and various grasses (e.g. *Calamagrostis canadensis*) are commonly found in the herb layer. White spruce stands have a very low understorey. Dominant species include: wild sarsaparilla, bunchberry, dewberry, grasses, twinflower, *Linnea borealis*, Labrador tea, *Ledum groenlandicum*, and various mosses (e.g. *Lycopodium annotinum, Pleurozium schreberi*).

Sites were distributed over four contiguous 10 x 10 km townships. Clearcutting of aspen stands in a portion of this area was conducted in the winter of 1993 and summer of 1994. Clearcut blocks alternated with uncut blocks and averaged 25 ha in size. There is no history of large scale deciduous logging in this region (Strong 1992). No site preparation took place on the blocks after harvest. Approximately 8% of the terrestrial land base was harvested and aspen and spruce stands make up another 67% of that land base. Clearcuts were covered by low vegetation (<1 m in height) consisting primarily of aspen and balsam poplar suckers, green alder and grasses and coarse woody debris (tree tops and limbs left over from logging operations).

During June, when sampling occurred, total precipitation was 149.4 mm in 1995 and 108.2 mm in 1996. Temperature maximums and minimums averaged 18.9 and 8.9°C in 1995 and 17.8 and 7.3°C in 1996 (B. Ralston, Alberta Environmental Protection, Land and Forest Service, pers. comm.). Weather measurements were taken at the Rock Island fire tower which was centrally located within my study site.

3.1.2 *Invertebrate sampling*

Invertebrates were sampled at the ground and shrub level to estimate the availability of forage for ground and foliage gleaning birds, respectively. Invertebrates were sampled in old aspen (80-130 y) stands adjacent to: (1) white spruce stands; (2) clearcut aspen stands;

and, (3) in the interior of old aspen stands. Interior sites were a minimum of 200 m from a cutblock edge and 100 m from a seismic line. Area of aspen stands averaged 124.1 ± 21.5 ha and ranged from 15.5 to 392.6 ha. For each treatment, 250 m long transects were set parallel with the forest edge. Eight transects/treatment were established in 1995; an additional transect/treatment was added in 1996 for a total of 9 transects/treatment. Locations of transects is shown in Appendix 3.1. Sites were selected so that each treatment had edges facing the same range of aspects (all major cardinal directions). Sampling stations were set at a random distance from the edge into the aspen stand, from 5 to 50 m away. Five sampling stations were set 50 m apart along each transect and randomly between 5-50 m from the edge into the aspen. The number of sampling stations per transect was based on sweep net and pitfall trap data collected in 1994 as follows: I sampled up to 9 stations per transect on a sub-sample of the transects used in 1995-6. Variation in biomass/sample along a transect tended to asymptote at 5 samples; therefore, I estimated that 5 samples were enough to adequately measure biomass within a transect (Appendix 3.2). At the shrub level, foliage around stations was sampled once using sweep nets (8 sweeps/station). At the ground level, pitfall traps were set out for one week to passively sample ground-dwelling invertebrates. A pitfall trap consisted of a 750 ml plastic tub with a 500 ml tub liner (after Spence and Niemelä 1994). Traps were buried up to the rim, flush with the ground, and filled with ethylene glycol. I used glycol because it killed and preserved invertebrates and it was less volatile than alcohol. Traps were open but covered by a wooden roof raised 4-5 cm over the trap rim to prevent rain from filling the traps. Pitfall traps were set 50 m apart so that depletion of local populations of invertebrates around a trap would not affect adjacent traps (Digweed *et al.* 1995). Sampling occurred over one week in mid-June and occured just as nestlings were beginning to hatch. Transects were sampled so that transects from all 3 treatments were sampled in a given day. I chose to sample using sweep nets and pitfall traps because both methods (1) were suitable for measuring relative abundance between treatments, (2) had a well-established methodology, and (3) were less time consuming and often as effective as other methods such as foliage-beating or litter sampling (Cooper and Whitmore 1990, Wolda 1990, Spence and Niemelä 1994).

Invertebrates were keyed to order and then in more detail if there were sufficient numbers. Identification keys in Borror *et al.* (1981) were used. Invertebrates were dried at 50°C for 24 h (after Zach and Falls 1979) and weighed to attain an average biomass per station per grid. The classification of groups composing the samples and their average biomass over 2 years is included in Appendix 3.3.

3.1.3 *Songbird surveys*

Density of songbirds at each type of edge was assessed by spot-mapping of male's territories from late May through June, i.e. when birds are settling onto territories until nestlings fledge (Verner 1985, Ralph *et al.* 1993). The timing of surveys focused mainly on monitoring migratory species and excluded most resident species. Approximately 5 ha grids were established in the same treatments described in the invertebrate sampling methods. Each grid followed the forest edge for 250 m and extended 150 m into the aspen habitat and 50 m into the adjacent habitat (see Appendix 2.2). (In interior sites, the entire grid was in aspen). I used 6 grids/treatment in the first year and 8 in the second. Therefore, invertebrates were measured in all spotmapping grids in 1995 and in all grids except one grid at aspen/clearcut and one grid at aspen/white spruce edge in 1996. In each treatment, there were mature and old aspen stands, with an average age of stand origin of 1920 and 1870, respectively. These stands reflected the average age of aspen stands in this region. In 1995, I used 2 mature and 4 old stands in each treatment and in 1996, I added 2 more mature stands to each treatment.

Grids were censused in fine weather by walking slowly along the transects laid parallel to the edge and 100 m into the aspen, and recording the species and location of singing males. Route direction and observers were alternated each visit. In each year, 3 observers surveyed the grids and one observer was constant between years. To help define territories, observers recorded additional information about songbird activity such as countersinging, calling, aggressive encounters, nest locations, carrying nest material or food. Censusing was conducted from dawn until 10 a.m., when avian activity was highest. Spot-mapping grids were censused approximately every 5-6 days, weather permitting, for a total of 6 rounds in

1995 and 7 rounds in 1996. Territories were defined by clustered records of singing males where a cluster had at least 2 records 10 days apart (Bibby *et al.* 1992). Territories that lay over a grid boundary and had equal registrations in and out of the grid were counted as half territories but no further subdivisions of territories took place.

Red-eyed Vireo was not reliably distinguished from Philadelphia Vireo by observers; therefore, I lumped these 2 species. Point count studies in the area indicate that Philadelphia Vireo is approximately 15 times less abundant that Red-eyed vireo (Schmiegelow *et al.* 1997). Nomadic species that travelled in flocks e.g. Pine Siskins and Cedar Waxwings were excluded from analyses.

3.1.4 *Vegetation sampling*

Vegetation structure and species composition were recorded within each transect using 0.04 ha plots and a protocol modified from the BBIRD program (Martin 1992). Plots were placed at each sampling station and averaged for the transect. Within each vegetation plot, the number, species and diameter at breast height (DBH) of trees and snags were recorded. Snag height was also recorded. Within a 0.008 ha nested sub-plot, number and species of saplings (DBH<2.5 cm) and poles (DBH 2.5-8 cm) were measured. Plots were divided into 4 quadrants, such that the dividing radii were perpendicular or parallel to the edge. At the 5 m point along each radius, using a 1 m^2 quadrat, data were collected on: ground cover (% of all green, shrub, forb, coarse woody debris, grass, dead grass and moss cover), and shrubs (number and species). Along each radius, number, diameter and length of coarse woody debris (CWD) were recorded. At each plot, average canopy height was recorded using a clinometer and canopy height was measured using a densiometer. Stand area and age were recorded from Alberta Vegetation Inventory or Phase 3 Forest Inventory maps.

3.1.5 *Statistical analysis*

The effect of edge type and year on invertebrate biomass per trap was tested using a nested analysis of variance with transect nested within edge type. For significant parameters, I ran multiple contrasts to determine which treatment(s) caused the effect. To correct for

multiple comparisons, I used joint Scheffé's confidence intervals to determine significance (Norüsis 1994). In all analyses, I set alpha to 0.10 because high variability in responses resulted in lower power to detect differences (Riffell *et al.* 1996). I also examined the effect of edge and year on the average biomass/sample of the major orders composing sweep net and pitfall trap samples using a nested analysis of variance. The same analysis was also performed on suborders or families of a particular order if it was a large component of the order. No invertebrate groups were included if the average biomass/sample was <0.50 mg in either year. All size classes of a group were included although for most groups, the vast majority of their biomass was in categories larger than 2 mm (Appendix 3.4 and 3.5). Many passerines are less likely to choose invertebrates smaller than this (Jansson and von Brömssen 1981, Guinan and Sealey 1987). Power analyses were perfomed for the nested analyses of variances within SPSS (Norüsis 1994). If power to detect a difference between means was low (<0.65) and effect size was large (d>0.2) (Cohen 1988), I used a randomization technique to test the effects of edge in each year. I used the computer program RANDCOMP 0.1 (Brzustowski 1997) which generates a statistical distribution of differences between treatments by repeatedly sampling from the observed data set. The program then tests the observed difference between the means of two treatments against the generated distribution of differences. If the fraction of the random distribution of differences that is greater than the observed difference is ≤ 0.10, then the observed difference is significant (at $\alpha \le 0.10$). The program was designed to test 2 groups; therefore, when I analysed the effect of edge, I calculated a mean invertebrate biomass per transect, and for each year, I performed 3 tests to compare all 3 treatments. I then adjusted the level of significance for multiple comparisons from $\alpha = 0.10$ to 0.02 (Zar 1984: p. 163).

I tested the relationship between (1) invertebrate abundance in sweep net samples and density of foliage-gleaning birds, and (2) invertebrate abundance in pitfall traps and density of ground-gleaning birds using linear regression analysis. For the former analysis, I used year as a covariate and in the latter, I analysed each year separately to determine if models were consistent between years. I looked at the effect of invertebrate abundance on density for songbird species recorded at territories in at least 6 grids over the 2 years of the study.

Variables were log-transformed where necessary to ensure normality. Stepwise multiple regression was used to determine whether average biomass/sample of individual invertebrate groups was related to songbird species density, regardless of edge type. Again, data from sweep net samples were entered into the regression for foliage-gleaning species and data from pitfall traps were entered for ground-gleaning species. For both guild types, biomass of Lepidoptera larvae, Homoptera, Diptera, Coleoptera, Arachneida, and Hymenoptera were entered into the regression as potential predictors of species density. These groups comprised the majority of both the sweep net and pitfall trap samples (see Appendix 3.3) and have all been reported in diet analyses of songbirds in other regions of North America (Stenger 1958, Zach and Falls 1978, Biermann and Sealey 1982, Robinson and Holmes 1982, Guinan and Sealey 1987, Van Horne and Bader 1990).

I performed ordination analyses using CANOCO 3.12 (ter Braak 1991) to determine whether invertebrate biomass was as important for predicting songbird densities as vegetation structure. Analyses were performed for both foliage- and ground-gleaning birds in both years. Selection of the appropriate ordination technique was determined using a detrended correspondence analysis to test the unimodality of the data (ter Braak 1995). Variables for vegetation structure, invertebrate biomass and dummy variables for each edge type were entered. Variables were standardized to mean zero with a standard deviation of 1 and highly collinear terms were eliminated from the analysis. The gradient length of the first axis was ≤1 standard deviation for both sampling protocols and in both years, therefore redundancy analysis (RDA), a linear technique, was used. The environmental variables used in the final model had significant canonical or regression coefficients based on their t-values for at least one of the first 2 axes and they also had the highest inter-set species-environment correlations (ter Braak 1995).

Stepwise multiple regressions were used to determine whether vegetation characteristics could predict invertebrate biomass. A reduced subset of all the vegetation variables was selected by (1) removing highly correlated variables, and (2) running single variable linear regressions on all the vegetation variables and eliminating variables with low explanatory power in both years ($R^2 < 0.05$). Some variables with low explanatory power in

the individual regressions were included if they were biologically relevant in other studies (e.g. leaf litter is important for many beetles (Niemelä and Spence 1994)). Means per transect were calculated for the following variables and these were entered into the model for sweep net data: dummy variables for edge type, canopy cover or volume of snags>12 cm DBH, litter depth, % leaf litter cover, % dead grass cover, % forb cover, shrub density, volume of CWD>11 cm DBH, basal area of deciduous trees, canopy height, stand age, stand area. Canopy cover and snag volume were highly correlated in 1995 (r=-0.7682). I ran models with either variable and included canopy cover in the final model because it resulted in a stronger (more significant slope, higher R^2) model. For pitfall trap data, the following variables were entered in the regression: dummy variables for edge type, litter depth, % litter cover, % dead grass cover, shrub density, number of CWD<11 cm DBH, volume of highly rotted CWD>11 cm DBH, number of deciduous saplings, basal area of deciduous trees, canopy cover, stand area and stand age.

Ordination analyses were performed, using the technique described above, to examine the effect of vegetation structure on the biomass of major invertebrate groups captured in sweep net and pitfall trap samples. Vegetation variables as well as dummy variables representing each edge type were entered into the RDA. Analyses were performed for both sweep net and pitfall trap samples in both years.

3.2. Results

3.2.1 *Effect of edge type and year on invertebrate biomass*

Invertebrate biomass measured with sweep nets was not significantly different between edge types (F=0.31, p=0.737, 1-β=0.169) but it was lower in 1996 (F=2.79, p=0.098, 1-β=0.503), (Figure 3.1a). There was also significant variation between transects (F=5.01, p<0.001, 1-β=1.000). Biomass in sweep nets ranged from an average (±SE) of 12.17 ± 2.44 to 94.77 ± 14.21 mg/sample between transects in 1995 and from 12.77 ± 2.83 to 71.36 ± 9.42 mg/sample between transects in 1996. For pitfalls traps, there was a significant interaction in invertebrate biomass between edge type and year (F=2.90, p=0.057, 1-

β=0.734), (Figure 3.1b). In both years, biomass at aspen/clearcut edges was significantly higher than interior sites (edge: t=1.83, CI=-0.03 to 0.35, edge*year: t=0.17, CI=-0.22 to 0.25). In 1995, biomass at aspen/white spruce edges was significantly higher than at interior sites; however, in 1996, there was no difference between these sites (edge: t=2.34, CI=0.005 to 0.29, edge*year: t=-2.10, -0.45 to 0.007). For aspen/clearcut vs. aspen/white spruce edges in 1995, biomass at aspen/white spruce edge was similar to that measured at aspen/clearcut edges but in 1996, biomass at aspen/white spruce edges was lower (edge: t=0.07, CI= -0.18 to 0.20, edge*year: t=2.32, CI=0.01 to 0.47). Again, there was significant variation between transects (F=1.51, p=0.081, 1-β=0.968). Biomass in pitfall traps ranged from an average (±SE) of 103.54 ± 20.20 to 605.98 ± 162.06 mg/sample between transects in 1995 and from 150.66 ± 18.12 to 624.56 ± 108.20 mg/sample between transects in 1996.

Response to edge by individual invertebrate groups composing sweep net and pitfall trap samples was not consistent between groups or years (Figure 3.2 and 3.3). For sweep net samples in 1995, biomass of lepidopterans and gastropods was significantly lower at the aspen/clearcut edge than in the interior or at aspen/white spruce edges (Figure 3.2 a-c). Biomass of homopterans was significantly higher at aspen/clearcut edges vs. within the interior of aspen stands. Biomass of Hymenoptera, Diptera and Brachycera, a sub-order within Diptera, was higher at aspen/clearcut edges than at either aspen/white spruce edges or the forest interior. Biomass of Cyclorrhapha was lower in the interior than at other sites. For sweep net samples in 1996, dipteran biomass was lower at aspen/white spruce edges than at other edge types (Figure 3.2 d-f). Biomass of brachyceran flies was again significantly higher at the aspen/clearcut edge than in the interior in 1996, but it was not different from the aspen/white spruce edge. Biomass of gastropods, homopterans and hymenopterans were significantly lower at clearcut edges than in the interior or at aspen/white spruce edges.

In pitfall traps in 1995, biomass of both Coleoptera and Carabidae was higher in the forest interior than at aspen/white spruce edges (Figure 3.3 a-c). Lepidopteran biomass was significantly lower at aspen/white spruce edges than in the interior or at aspen/clearcut edges. Biomass of arachnids was significantly lower in the interior versus either edge type.

Biomass of hymenopterans and homopterans was significantly higher at the aspen/clearcut edge than within the forest interior. In 1996, no differences in biomass of Coleoptera between edge types were observed (Figure 3.3. d-f). Results for lepidopterans mirrored results found in 1995. Biomass of arachnids and hymenopterans was significantly higher at aspen/clearcut edges than in both the interior and aspen/white spruce edges. Homopteran biomass was lower at aspen/clearcut edges than at aspen/white spruce edges. No differences in biomass among treatments were observed for the remaining invertebrate groups in 1996.

Many invertebrate groups declined overall in 1996 from levels in the previous year although results were sometimes different between sampling techniques (Table 3.1). Biomass of lepidopterans and gastropods declined in 1996 in both sweep net and pitfall trap samples. Biomass of dipterans in sweep nets increased in 1996, due to an increase in Nematocera, while biomass of dipterans in pitfall traps declined due to a decrease in Cyclorrapha. Homopteran biomass decreased in sweep net samples and hymenopteran biomass decreased in pitfall trap samples in 1996. Coleopteran biomass remained similar between years in both sweep net and pitfall trap samples although both carabid and staphylinid biomass increased from 1995 to 1996.

3.2.2. *Effect of invertebrate biomass on songbird density*

There was no relationship between invertebrate abundance in sweep nets and the density of foliage-gleaning songbirds (F=0.42, p=0.661, R^2<0.01, Figure 3.4a). Although densities of ground-gleaning birds were significantly lower in the second year (Chapter 2), there was no relationship between their densities and invertebrate abundance in pitfall traps (overall model: F=6.18, p=0.005, R^2=0.21, invertebrate abundance: t=-0.603, p=0.550, Figure 3.4b). Analyses of individual species reflected community level results except for Yellow-rumped Warbler (Table 3.2). However, for this species, density was inversely related to invertebrate biomass (β=-0.0576). For all other foliage- and ground-gleaning species, there was no significant relationship between density and invertebrate biomass.

Regressions of the major invertebrate groups with songbird species density did not reveal similar relationships between years (Table 3.3). Biomass of Lepidoptera larvae

predicted Red-eyed Vireo and Black-throated Green Warbler densities in both 1995 and 1996 but relationships were opposite between years (i.e. a positive relationship in one year and a negative relationship in another). Biomass of Lepidoptera larvae was the most frequent predictor of species density. For ground-gleaning species, only Coleoptera predicted density of Ovenbirds in 1996. Where significant relationships were found, invertebrate biomass explained from 9-40% of variation in songbird species density.

When analysed together, vegetation variables were better predictors of songbird density in ordination analyses than invertebrate biomass. For foliage-gleaning species, similar models predicted densities in both years: basal area of coniferous trees, canopy cover and number of deciduous poles were important predictors of density in 1995 and basal area of coniferous trees, stand age, number of deciduous poles and grass cover were important in 1996 (Table 3.4, Figure 3.5). Stand age and canopy cover were correlated, particularly in 1995 (r= -0.7849 in 1995, r= -0.5641 in 1996). In 1995, eigenvalues for the RDA were 0.295 for Axis 1 and 0.156 for Axis 2. The biplot explained 45.1% of the variance in songbird density and 96.9% of the relationship between songbirds and the environmental variables. In 1996, eigenvalues for the RDA were 0.363 for Axis 1 and 0.161 for Axis 2. The biplot explained 52.3% of the variance in songbird density and 92.3% of the relationship between songbirds and the environmental variables. For ground-gleaning species, different vegetation variables predicted densities between years: volume of large CWD, canopy cover and leaf litter cover were significant in 1995 while stand age and forb cover were important in 1996 (Table 3.4, Figure 3.6). In 1995, eigenvalues for the RDA were 0.630 for Axis 1 and 0.039 for Axis 2. The biplot explained 66.9% of the variance in songbird density and 99.3% of the relationship between songbirds and the environmental variables. In 1996, eigenvalues for the RDA were 0.386 for Axis 1 and 0.41 for Axis 2. The biplot explained 42.7% of the variance in songbird density and 100% of the relationship between songbirds and the environmental variables.

3.2.3 *Vegetative predictors of invertebrate biomass*

Different factors predicted total biomass in sweep net samples between years (Table 3.5). Biomass increased with increasing basal area of deciduous trees and volume of highly rotted CWD>11 cm DBH and decreasing % cover of leaf litter in 1995. In 1996, biomass increased with increasing % cover of dead grass and decreasing basal area of deciduous trees, stand age and stand area. Different models were also generated for pitfall trap samples in either year (Table 3.5). In 1995, increasing biomass of pitfall trap samples was predicted by increasing stand age and canopy cover and decreasing dead grass and % cover of leaf litter. This relationship did not hold in 1996; biomass in pitfall traps was inversely related to shrub density.

Vegetation variables also predicted the biomass of the most abundant invertebrate groups captured in sweep net samples but again, relationships were not constant between years. In sweep net samples, number of deciduous poles, basal area of deciduous trees, volume of CWD>11 cm DBH and presence of aspen/clearcut edge were the strongest predictors of biomass of the major invertebrate groups in 1995 (Table 3.6). For sweep net samples in 1995, biomass of Arachneida, Homoptera, Hemipteran, Coleoptera and Diptera was positively related with vegetation variables associated with increasing vertical heterogeneity, i.e. deciduous poles, basal area of deciduous trees and volume of CWD>11 cm DBH (Figure 3.7a). Gastropoda was negatively associated with the same variables. Biomass of Hymenoptera was positively related to presence of aspen/clearcut edge while biomass of Lepidoptera larvae was negatively related to aspen/clearcut edge. In 1996, biomass of invertebrate groups captured in sweep nets was predicted by number of deciduous saplings, number of snags <12 cm DBH, % cover of dead grass, stand area and stand age (Table 3.6). Dead grass cover was highly correlated with grass (r=0.8779) and leaf litter cover (r=-0.7093) in 1996. Biomass of Arachneida, Homoptera, Coleoptera, Diptera and Hymenoptera was related to increasing cover of dead grass and decreasing stand age (Figure 3.7b). Only biomass of Hemiptera was still positively associated with increasing understorey development, i.e. deciduous saplings. Biomass of Lepidoptera larvae

was positively associated with larger aspen stands and increased number of deciduous saplings and negatively associated with number of snags <12 cm DBH.

In 1995, the eigenvalues for the RDA of invertebrates captured by sweep nets were 0.198 for Axis 1 and 0.165 for Axis 2. The biplot explained 36.3% of the variance in biomass of invertebrates and 90.7% of the relationship between invertebrates and the vegetation variables. In 1996, the eigenvalues were 0.213 for Axis 1 and 0.068 for Axis 2. Here, the biplot explained 28.1% of the variance in invertebrate biomass and 80.9% of the relationship between invertebrates and the vegetation variables.

Biomass of major invertebrate groups captured by pitfall traps was predicted by number of deciduous poles, volume of snags>12 cm DBH, litter depth and % cover of CWD in 1995 and by shrub density, number of coniferous poles, volume of snags >12 cm DBH and presence of aspen/clearcut edge in 1996 (Table 3.6). In 1995, biomass of Hymenoptera was strongly associated with litter depth and % cover of CWD (Figure 3.8a). Biomass of Diptera and Coleoptera were negatively associated with number of deciduous poles and the volume of snags > 12 cm DBH while Gastropoda, Arachneida and most strongly, Lepidoptera larvae, were positively associated with these variables. In both years, Homoptera was found close to the origin so no variables predict this group (Figure 3.8a-b). Presence of aspen/clearcut edge predicted biomass of Hymenoptera and Arachneida in 1996 (Figure 3.8b). Biomass of Lepidoptera larvae was strongly associated with volume of snags>12 cm DBH while Diptera was negatively associated with the same variable. Biomass of Coleoptera was negatively related with shrub density and number of coniferous poles.

In 1995, the eigenvalues for the RDA of invertebrates captured by pitfall traps were 0.282 for Axis 1 and 0.138 for Axis 2. The biplot explained 42.0% of the variance in biomass of invertebrates and 91.9% of the relationship between invertebrates and the vegetation variables. In 1996, the eigenvalues were 0.234 for Axis 1 and 0.115 for Axis 2. Here, the biplot explained 35.0% of the variance in invertebrate biomass and 94.9% of the relationship between invertebrates and the vegetation variables.

3.3 Discussion

3.3.1. *Invertebrate response to forest edges*

Invertebrate biomass was not higher at aspen/clearcut edges than aspen/white spruce edges or the forest interior, when sampled by sweep nets. In 1995, only a few groups responded to edge type but the response was consistently to aspen/clearcut edge. Lepidoptera larvae, the most abundant group composing sweep net samples in 1995 were actually lower at aspen/clearcut edges than at other edge types. Lepidopteran larvae may have developed poorly at this edge type, or more probably, they may have developed so quickly that they had already pupated by the time I sampled. Increased insolation and higher temperatures resulting in earlier bud burst and higher food quality at the aspen/clearcut edge could have contributed to faster development times. Biomass of Hymenoptera was also higher at the aspen/clearcut edge than at aspen/white spruce edges and the forest interior, and this result also applies to parasitic wasps within this group (interior: 0.62 ± 0.15 mg/sample; aspen/clearcut: 1.05 ± 0.31 mg/sample; aspen/white spruce: 0.54 ± 0.12 mg/sample). Emergence of parasitoids may have occurred earlier if hosts were available earlier and development times were shorter at the aspen/clearcut edge than at other sites. However, samples needed to be identified to the species level to verify this speculation. No other groups showed a difference in biomass between edge types although there may have been changes in species composition (e.g. Didham 1997).

In 1996, temperatures in June averaged slightly more than 1°C colder than in 1995 which could have had a strong effect on invertebrate development (Gullan and Cranston 1994). Total biomass in sweep net samples in 1996 dropped considerably from levels measured in 1995, especially for Lepidoptera and Homoptera. The effect of the cooler temperatures may have negated the benefit of the aspen/clearcut edge for invertebrate biomass. In 1996, there was no difference in biomass of Lepidoptera larvae between edge types and Hymenoptera, Gastropoda and brachycerid flies were lower at the aspen/clearcut edge than the forest interior. If insolation and temperature were higher at the aspen/clearcut

edge, no significant benefit was accrued with respect to overall biomass by invertebrates inhabiting that edge in 1996.

Response of invertebrates caught in pitfall traps to edge type was different in each year. In both years, biomass of invertebrates captured in pitfall traps was lower in the forest interior than at the aspen/clearcut edge. In 1995, biomass at aspen/white spruce edges was higher than in the interior while in 1996, it dropped to a level lower than that found at the aspen/clearcut edge but similar to levels measured in the interior. This effect of aspen/white spruce on biomass contrasts with observations of decreased biomass of ground dwelling invertebrates from deciduous to mixed-wood to conifer stands by Smith and Schugart (1987). Smith and Schugart (1987) suggested that the acidity of the litter layer around conifer reduced habitat suitability for these invertebrates. Although biomass was not lower at aspen/white spruce edges than the stand interior, species composition could have differed as soil drainage changed (Strong 1992, Niemelä and Spence 1994, Song unpubl. data). The aspen/white spruce edge does not appear to be a poorer location than the forest interior for birds to forage for most invertebrate groups.

3.3.2 *Songbird response to invertebrate biomass*

Higher biomass of all invertebrates did not lead to higher densities of songbirds. Biomass of individual invertebrate groups was a better predictor of density for a few songbird species but for most, there was no relationship at all or the relationship was not strong. Also, for some species, the relationship between invertebrate biomass and species density was negative. For any given species, the relationship between species density and invertebrate biomass changed between years. However, these changes were not reflected by differences in invertebrate biomass between years. For example, Red-eyed Vireo, Mourning Warbler, Winter Wren, Canada Warbler and Chipping Sparrow had a positive relationship with biomass of Lepidoptera larvae in 1996 where no relationship or a negative relationship existed in the year before. But, biomass of larvae actually decreased in 1996 from levels in 1995. I would have expected less reliance on Lepidoptera larvae by birds in 1996 if biomass was lower. Birds often switch from preferred species to other prey types when availability of

a preferred food decreases (e.g. Zach and Falls 1978, Busby and Sealey 1979). Alternatively, birds may have been reluctant to use other types of prey if they had lower nutritional value or were more difficult to handle (Zach and Falls 1978, Robel *et al.* 1995). Possibly Lepidoptera larvae were superabundant in 1995 and a relationship between biomass and bird density only appeared as Lepidoptera larvae became limiting in 1996.

Differences in densities of songbird species between edge types shown in Chapter 2 did not correlate with differences in invertebrate biomass between edge types. For example, Hermit Thrush, Warbling Vireo, Red-eyed Vireo, and Rose-breasted Grosbeak had lower densities at aspen/white spruce edges compared to other edge types (Chapter 2). Either there was no relationship between invertebrate biomass and bird density for these species, or the invertebrate group that predicted their density did not have a negative response to aspen/white spruce edge vs. other sites.

There are a number of reasons, both biological and methodological, that could explain why invertebrate biomass had no consistent effect on songbird densities. Vegetation structure had a much stronger effect on songbird density and is probably more important for determining territory location and size. Food may be a more important determinant of density in systems where habitat is less heterogeneous than the boreal forest. Also, as previously suggested, if food is generally superabundant in the boreal forest, a relationship between density and food supply would not be expected (Schoener 1968). In Burke and Nol's (1998) study of Ovenbirds, their unoccupied sites had invertebrate biomasses 30 times lower than occupied sites on average. In my study, biomass in pitfall traps did not vary nearly as much among transects (see Figure 3.1a). Stronger relationships between songbird density and invertebrate biomass may have appeared in my study if there were more dramatic differences in biomass between sites. From a methodological standpoint, I did not sample directly on specific songbird territories but only within the grid. If birds were responding to more subtle variation at smaller scales than at the stand level, my study design would not have detected this. Burke and Nol (1998) found a relationship between invertebrate abundance and Ovenbird presence by comparing samples taken directly on the Ovenbird territory and at random sites off the territory. This lack of precision in my design,

aimed at the community level, may be a shortcoming of this study. I also did not sample in the canopy where birds may also forage. Dynamics of canopy level invertebrates may differ from those in lower strata (e.g. Hammond *et al.* 1997) and could have had an influence on my results.

Components of songbird life history may have been affected by differences in invertebrate abundance between edges and the interior, even if their densities were not. Effects of food supply on fecundity of passerine birds are well-documented (review in Martin 1987). Blancher and Robertson (1987) showed that increases in invertebrate abundance increased clutch initiation date, clutch size, nestling growth and decreased time between feedings but had no effect on abundance of 2 species of kingbird. Therefore, differences in invertebrate biomass between edge types could still affect songbirds. For example, if caterpillars developed more quickly at the aspen/clearcut edge than at other sites in 1995, then they would have been available as a prey source for a shorter time here also. Lepidoptera larvae form the major component of many songbird's diets, especially foliage-gleaning birds (Biermann and Sealey 1982, Robinson and Holmes 1982, Holmes and Schultz 1988, Grundel and Dahlstein 1991, Rodenhouse and Holmes 1992, Sample *et al.* 1993); therefore, there may have been some ramifications for reproductive success of songbirds at aspen/clearcut edges in 1995.

3.3.3. *Influence of vegetation on invertebrate biomass*

Vegetation structure predicted invertebrate biomass but specific predictors changed between years. Changes in climate may have been a confounding factor that limited the predictive ability of vegetation. Models were moderately strong, especially for the regression model of total invertebrate biomass where vegetation explained up to 46% of variation. Ordination analyses explained similar amounts of variation, from 28.1 to 42%.

Invertebrate biomass was not always positively related to vertical heterogeneity or understorey complexity. Increasing density of shrubs, saplings or poles did not predict increasing total biomass for either sweep net or pitfall trap catches. In ordination analyses of community pattern, measures of understorey complexity e.g. shrub density, coniferous or

deciduous poles, deciduous saplings, were important predictors although, again, the relationship with biomass of specific groups was not always positive. Older aspen stands, which tend to have much more vertical heterogeneity than mature stands (Chapter 2, Lee *et al*. 1995), did not have greater invertebrate biomass except for pitfall trap captures in 1995. In sweep net samples in 1996, biomass was inversely related to stand age. Stand age was a significant predictor in some of the ordination analyses but no invertebrate group was closely associated with it. Therefore, the idea that songbirds are attracted to areas of higher vertical heterogeneity because of higher food availability does not seem to hold true. My results are consistent with those of Spence *et al*. (1997), who found that carabid abundance tended to be slightly lower in older aspen stands than mature stands. Invertebrate development is affected by factors such as type and amount of food, humidity, temperature, secondary plant chemicals, and predators and parasites (Gullan and Cranston 1994) and all these factors may interact to confound predictions about absolute biomass in any one habitat type.

Smith and Schugart (1987) suggested that songbirds may use "structural cues" from vegetation when selecting their territories in the spring as a way to estimate invertebrate abundance later in the season. If invertebrate abundance is not reliably predicted by the same, or at least similar, vegetation features every year, this would not be a reliable method of estimating food supply for birds in the boreal forest. Further, if invertebrates respond more quickly than vegetation to changes in microclimate at clearcut edges, birds would not be able to detect these change in food supply using vegetation cues.

3.3.4 *Conclusions*

Invertebrate availability for birds, as measured by biomass, varied between edge types but no consistent effect on songbird density was observed. Vegetation structure was more important for determining songbird densities than invertebrate biomass. Superabundance of food for birds could also explain the lack of a relationship between bird density and invertebrate biomass. Vegetation structure predicted invertebrate biomass but predictor variables varied between years. Before the effect of invertebrate availability on songbirds is

discounted, further study is needed to determine whether invertebrate biomass has ramifications for foraging behaviour and reproductive success.

Table 3.1. Composition of (a) sweep net and (b) pitfall trap samples in 1995 and 1996 in mg. Only groups that averaged at least 0.50 mg/sample are included.

(a) Sweep net samples

| Group | Biomass (mg) | | | |
	1995	1996	F	p
Lepidoptera	15.06	6.82	10.22	0.002
Lepidoptera larvae	14.67	6.80	8.67	0.004
Diptera	6.25	12.08	48.54	<0.001
Cyclorrhapha	3.71	2.36	20.80	<0.001
Nematocera	1.35	8.38	211.15	<0.001
Brachycera	1.19	1.05	0.02	0.892
Homoptera	6.15	4.51	19.19	<0.001
"Hoppers"	5.68	4.35	14.34	<0.001
Coleoptera	5.60	5.74	1.83	0.179
Arachneida	3.47	4.57	0.02	0.880
Hymenoptera	1.44	1.49	0.66	0.418
Hemipteran	1.15	0.61	14.79	<0.001
Gastropoda	0.92	0.85	2.86	0.094

(b) Pitfall trap samples

| Group | Biomass (mg) | | | |
	1995	1996	F	p
Coleoptera	159.11	199.45	1.74	0.190
Carabidae	131.10	166.87	3.63	0.060
Staphylinidae	18.43	24.35	4.42	0.038
Diptera	94.78	61.28	4.68	0.033
Cyclorrhapha	93.68	56.21	8.08	0.005
Lepidoptera	10.56	1.83	37.20	<0.001
Lepidoptera larvae	9.75	1.58	39.63	<0.001
Hymenoptera	9.04	3.01	0.22	0.637
Arachneida	8.07	46.98	211.92	<0.001
Homoptera	1.74	1.30	2.15	0.146
Gastropoda	3.34	0.87	26.47	<0.001

Table 3.2: Relationship between invertebrate biomass and density of songbird species. Biomass in sweep net samples is related to density of foliage-gleaning species and biomass in pitfall traps is related to density of ground-gleaning species. Values in parentheses are t-values. Year was included as a covariate. Results of overall model are reported if year was non-significant otherwise results are reported only for invertebrate abundance. R² is for entire model. Sample size, n, indicates the number of grids over 2 years that had territorial birds. See Appendix 2.3 for scientific names.

Songbird species	n	adjusted R²	F or (t)	p
Foliage-gleaners				
Swainson's Thrush (SWTH)	12	<0.01	0.37	0.696
Solitary Vireo (SOVI)	6	0.02	1.36	0.270
Warbling Vireo (WAVI)	6	0.01	1.16	0.324
Red-eyed Vireo (REVI)	35	<0.01	0.35	0.707
Tennessee Warbler (TEWA)	39	0.22	(1.16)	0.251
Yellow Warbler (YWAR)	11	<0.01	0.23	0.795
Yellow-rumped Warbler (YRWA)	29	0.24	(-1.68)	0.101
Black-throated Green Warbler (BGNW)	22	0.03	1.54	0.227
American Redstart (AMRE)	16	0.01	1.11	0.338
Mourning Warbler (MOWA)	35	0.02	1.41	0.257
Western Tanager (WETA)	15	<0.01	1.02	0.382
Rose-breasted Grostbeak (RBGR)	18	0.14	(-.84)	0.407
Ground-gleaners				
Winter Wren (WIWR)	13	0.05	2.03	0.145
Hermit Thrush (HETH)	7	<0.01	0.27	0.767
Ovenbird (OVEN)	35	<0.01	1.07	0.352
Connecticut Warbler (COWA)	12	<0.01	0.16	0.849
Canada Warbler (CAWA)	8	<0.01	0.21	0.808
Chipping Sparrow (CHSP)	22	<0.01	0.84	0.440
White-throated Sparrow (WTSP)	33	0.03	1.56	0.223

Table 3.3. Results of stepwise linear regressions of songbird density and biomass of invertebrate groups in 1995 and 1996. See Appendix 2.3 for species codes.

Songbird species	1995 Equation	R^2	p	1996 Equation	R^2	p
Foliage-gleaners						
SWTH	0.067-0.007(Diptera)	0.11	0.093	no model fit		
SOVI	no model fit			-0.005 + 0.002 (Arachneida)	0.15	.037
WAVI	no model fit			no model fit		
REVI	0.23-0.005(Lep. larvae)	0.30	0.011	0.09 + 0.094(Lep. larvae)	0.13	0.048
TEWA	0.10 + 0.003(Lep. larvae)	0.11	0.10	no model fit		
YWAR	no model fit			0.09 - 0.005 (Diptera)	0.14	0.045
YRWA	no model fit			no model fit		
BGNW	0.027 + 0.004 (Lep. larvae) - 0.008 (Coleoptera)	0.45	0.004	0.028 - 0.004 (Lep. larvae) + 0.10 (Arachneida)	0.32	0.008
AMRE	0.008 + 0.014 (Coleoptera)	0.19	0.042	no model fit		
MOWA	0.06 +0.01 (Diptera)	0.12	0.084	0.07 + 0.008 (Lep. larvae) - 0.016 (Hymenoptera)	0.23	0.061
WETA	0.081 - 0.011 (Arachneida)	0.12	0.089	no model fit		
RBGR	no model fit			no model fit		
Ground-gleaners						
WIWR	no model fit			0.03 + 0.003 (Lep. larvae) - 0.015 (Homoptera)	0.18	0.054
HETH	no model fit			no model fit		
OVEN	no model fit			0.07 +0.0003 (Coleoptera)	0.13	0.053
COWA	no model fit			no model fit		
CAWA	no model fit			0.009 + 0.002 (Lep. larvae)	0.09	0.086
CHSP	no model fit			0.059 + 0.004 (Lep. larvae) - 0.0005 (Diptera)	0.40	0.003
WTSP	no model fit			no model fit		

Table 3.4. Canonical coefficients and inter-set correlations for vegetation and invertebrate groups that predicted songbird density. Results are reported for the first two axes only. * indicates significance based on t-values at $p \leq 0.10$.

Year	Variable	Canonical coefficients		Inter-set correlations	
		Axis 1	Axis 2	Axis 1	Axis 2
Foliage-gleaning birds					
1995	Basal area of coniferous trees	-0.5716*	0.8622*	-0.5619	0.6619
	Canopy cover	-0.5679*	-0.3257	-0.6265	-0.4846
	Deciduous poles	0.3073	0.4356*	0.6437	0.3356
1996	Basal area of coniferous trees	-0.0387	0.6263*	-0.2653	0.7493
	Stand age	-0.0575	0.6464*	0.5588	0.5942
	Deciduous poles	0.6121*	-0.1904	0.7842	-0.0219
	Grass cover	0.5810*	-0.0600	0.7622	0.1318
Ground-gleaning birds					
1995	Volume of large DWD	-0.0617	0.9253*	-0.6004	0.2948
	Canopy cover	0.8426*	1.1415*	0.9304	0.1097
	Leaf litter cover	0.2090	-0.8421	0.6014	-0.3552
1996	Stand age	0.6226*	0.7938	0.5985	0.3458
	Forb cover	-0.7043	0.7223	-0.6577	0.3057

Table 3.5 Stepwise multiple regression models predicting average invertebrate biomass of sweep net and pitfall trap captures from vegetation characteristics.

Year	Model	Adjusted R^2	F	p
Sweep net samples				
1995	1.18 - 0.017(Leaf litter) + 0.58(Area of Deciduous Trees) + 0.093(Volume of Large DWD)	0.42	6.47	0.0031
1996	1.72 + 0.032(Dead Grass) - 0.26(Area of Deciduous Trees) - 0.25 (Stand Age) + 0.00052(Stand Area)	0.46	6.44	0.0014
Pitfall trap samples				
1995	2.16 - 0.020(Leaf litter) - 0.056 (Dead Grass) + 0.238 (Stand Age) + 0.009 (Canopy Cover)	0.43	5.380	0.0046
1996	2.56 - 0.029 (Shrub Density)	0.11	4.060	0.0548

Table 3.6. Canonical coefficients and inter-set correlations for vegetation variables used in redundancy analysis of invertebrate data. Results are reported for the first 2 axes only. * indicates significance based on t-values at $p \leq 0.10$.

Year	Variable	Canonical coefficients		Inter-set correlations	
		Axis 1	Axis 2	Axis 1	Axis 2
Sweep net samples					
1995	Aspen/clearcut edge	-0.7470*	0.6270*	-0.4767	0.5603
	Basal area of deciduous trees	0.4319*	0.5989*	0.2036	0.2533
	Deciduous poles	0.5417*	0.5373*	0.2837	0.5036
	Volume of large DWD	0.4541*	0.0604	0.4053	0.0801
1996	Stand age	0.8652*	0.2852	0.2196	-0.0891
	Stand area	-0.5584*	0.1976	-0.2927	-0.1642
	Deciduous saplings	0.3686	-1.0107*	-0.0308	-0.5228
	Dead grass cover	-0.7995*	0.4544	-0.3849	-0.0389
	Small snags	0.4333	0.6147	0.2260	0.3393
Pitfall trap samples					
1995	Stand age	0.5525*	0.4446*	0.1320	0.3344
	DWD cover	0.4993*	-0.6193*	0.3934	0.0680
	Deciduous poles	-0.3782	1.0570*	-0.1227	0.6552
	Litter depth	0.6803*	0.4479*	0.5573	.1525
	Volume of large snags	-0.4119*	-0.2152	-0.3017	.1812
1996	Aspen/clearcut edge	0.7590*	0.0190	0.6722	-0.1813
	Coniferous poles	-0.0165	0.5514*	-0.2209	-0.3664
	Shrub density	-0.1816	0.5452*	-.1658	0.5181
	Volume of large snags	0.5100*	0.4841	0.4120	0.4662

Figure 3.1. Effect of edge type and year on average biomass per sample (mg) in (a) sweep nets and (b) pitfall traps. Difference of at least one letter indicates significance (p<0.10) between edge types in a given year.

(a) Sweep net

(b) Pitfall trap
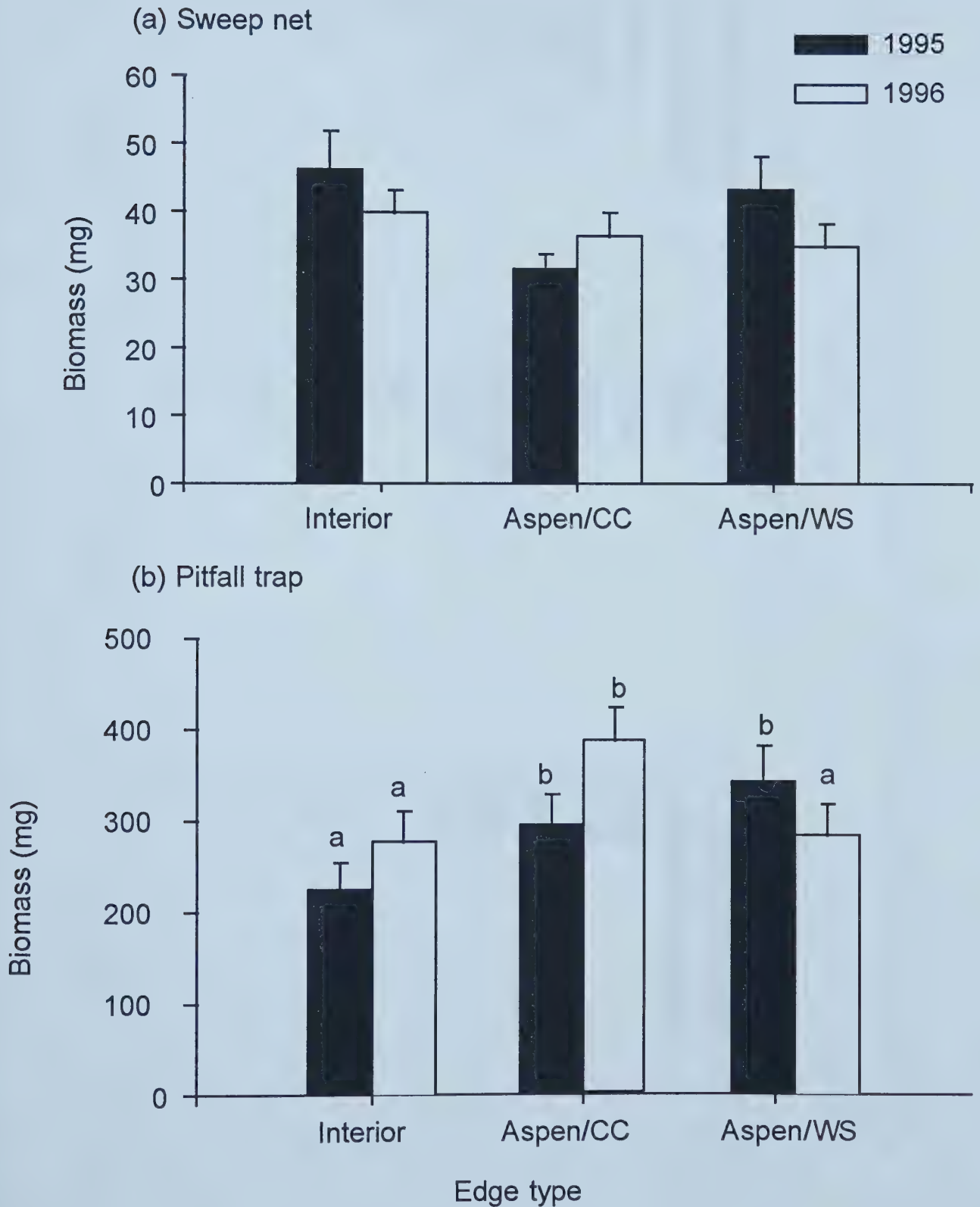
Figure 3.2. Effect of edge type on average biomass/sweep net sample of invertebrate groups in (a-c) 1995 and (d-f) 1996. Results are reported for invertebrate orders that composed >0.50 mg/sample on average for a given year and for families or suborders, if they contributed sustantially to the sample. Difference of one letter indicates significance at p<0.10.

a) Interior 1995

b) Aspen/Clearcut 1995

c) Aspen/White spruce 1995

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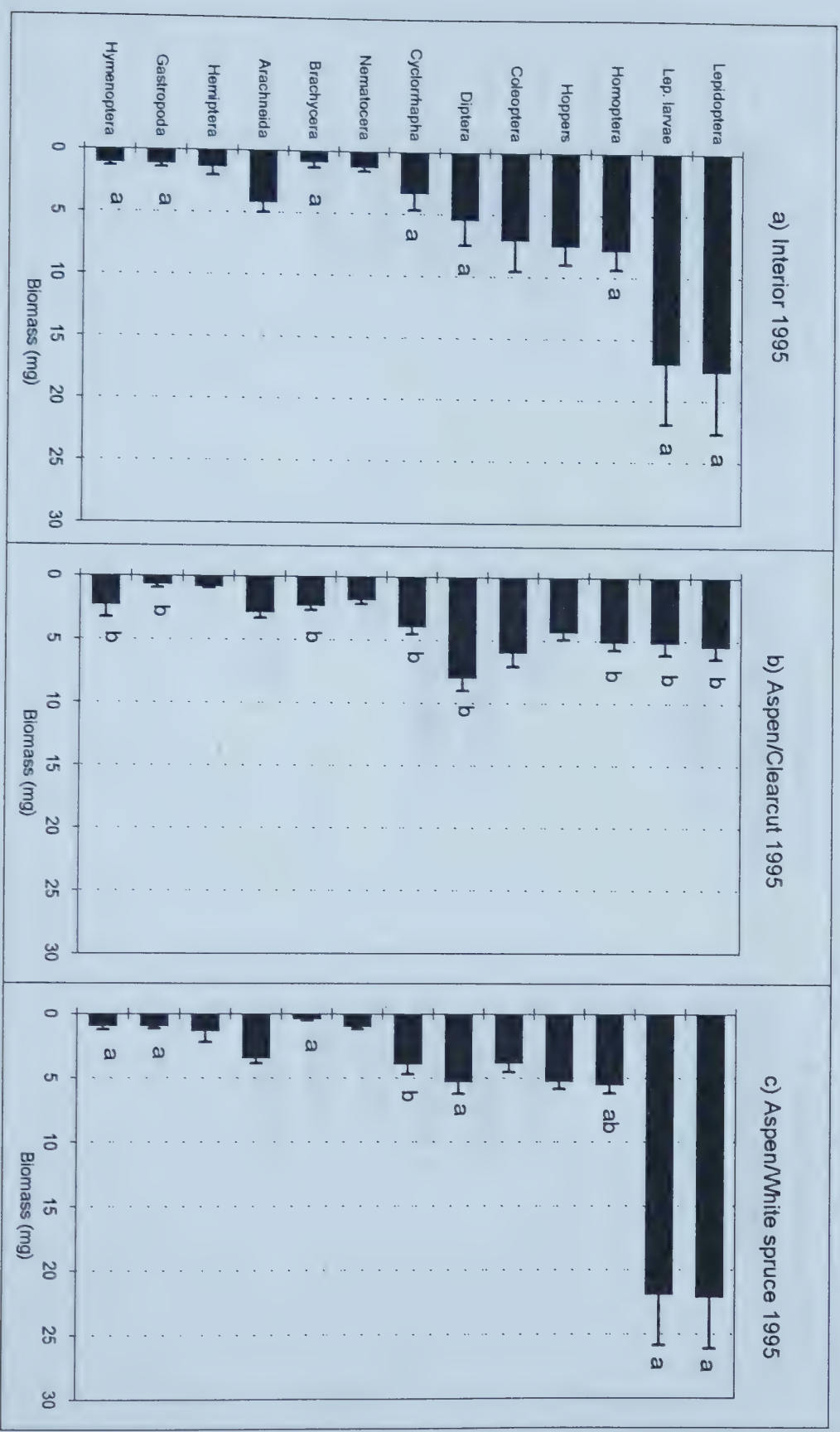
Figure 3.2 continued.

Figure 3.3. Effect of edge type on average biomass/pitfall trap sample of invertebrate groups in (a-c) 1995 and (d-f) 1996. Results are reported for invertebrate orders that composed >0.50 mg/sample on average for a given year and for families or suborders, if they contributed sustantially to the sample. Difference of one letter indicates significance at p<0.10.

Figure 3.3 continued.

d) Interior 1996

e) Aspen/Clearcut 1996

f) Aspen/White spruce 1996
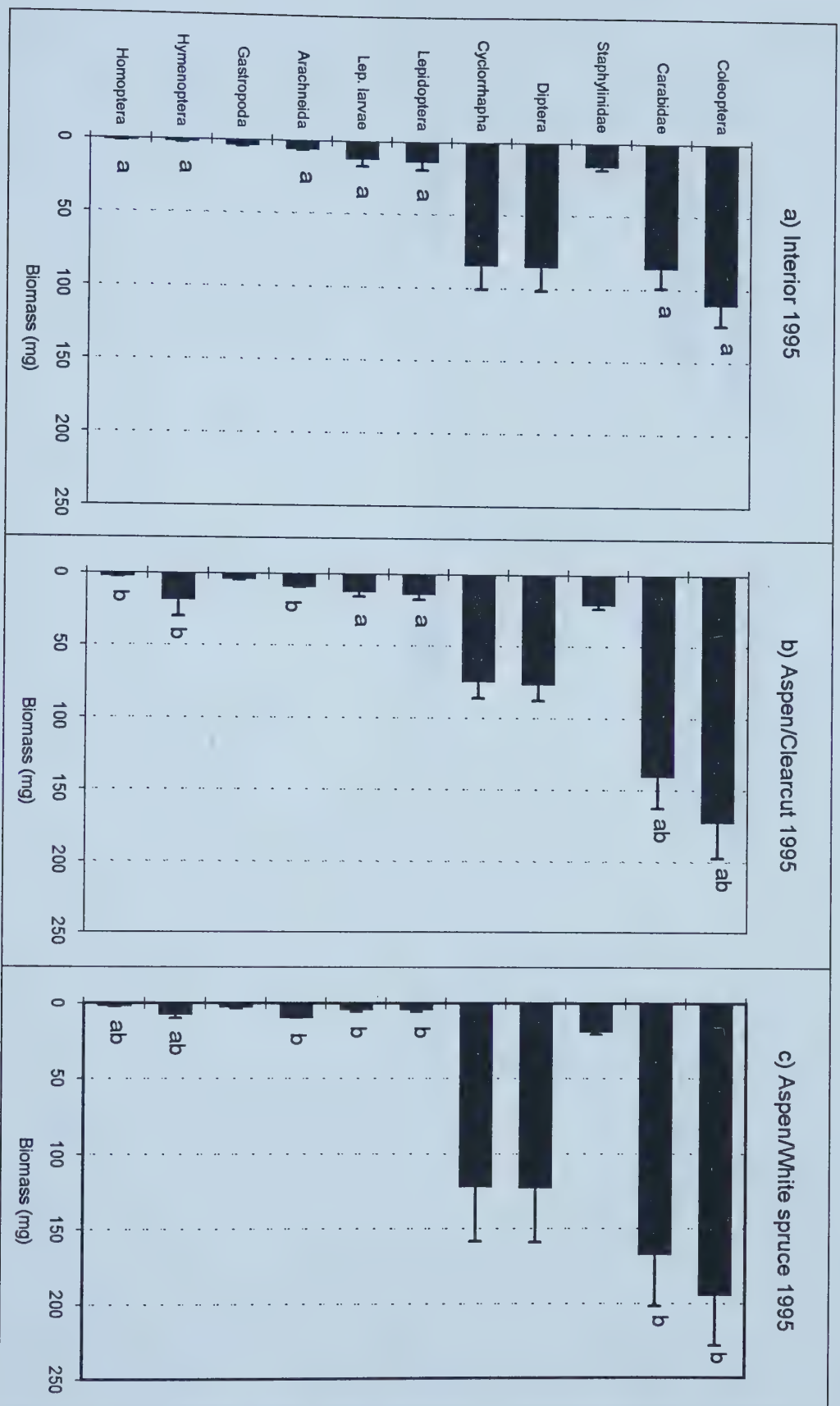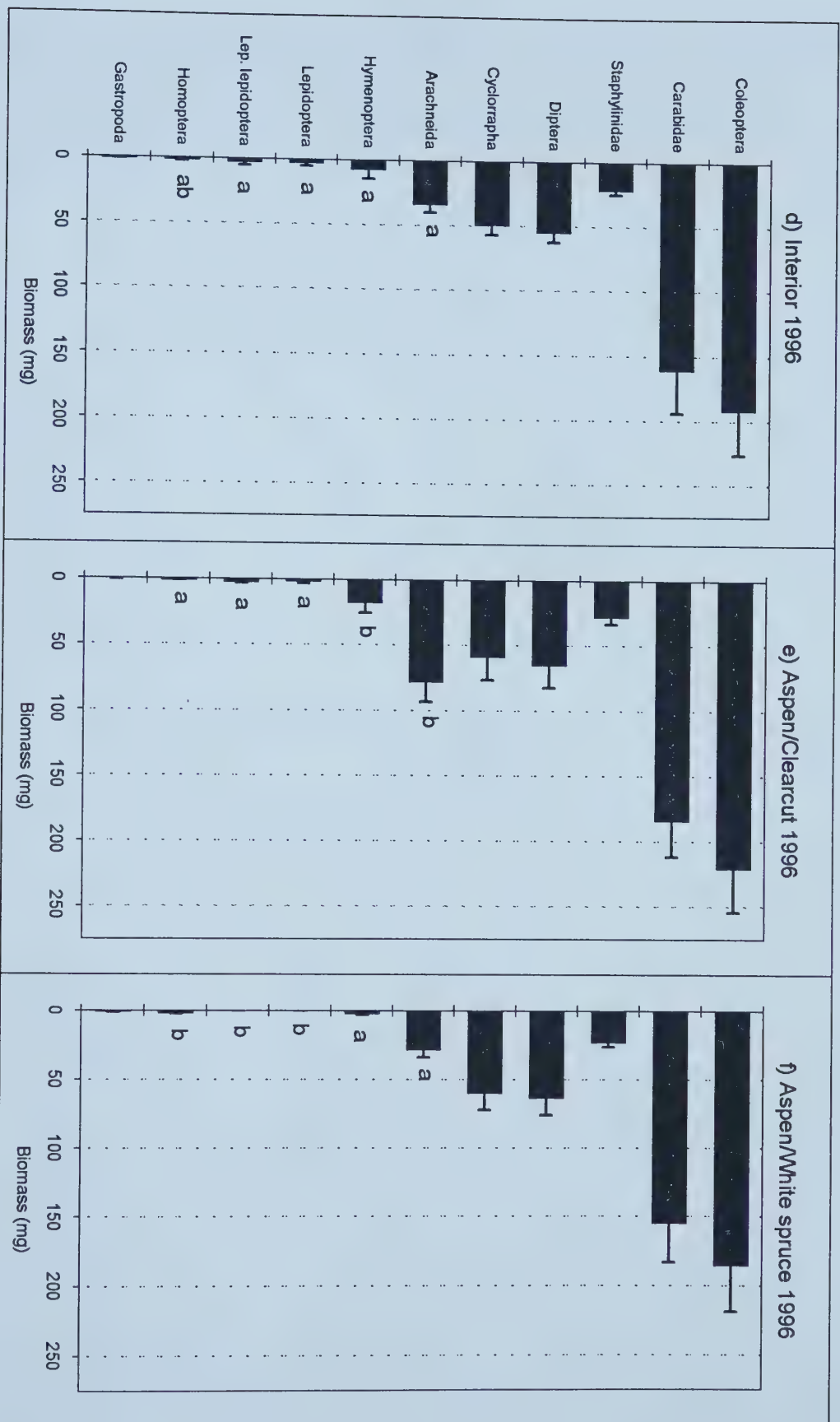
Figure 3.4. No significant relationship existed between (a) density foliage-gleaning birds and average biomass/sample of sweep net samples (F=0.419, p=0.661, R-squared<0.01) or between (b) density ground-gleaning birds and average biomass/sample of pitfall traps (Overall model: F=6.18, p=0.005, R=squared=0.21, for invertebrate biomass: t=-0.603, p=0.550). Data were from 1995 and 1996 and year was used as a covariate.
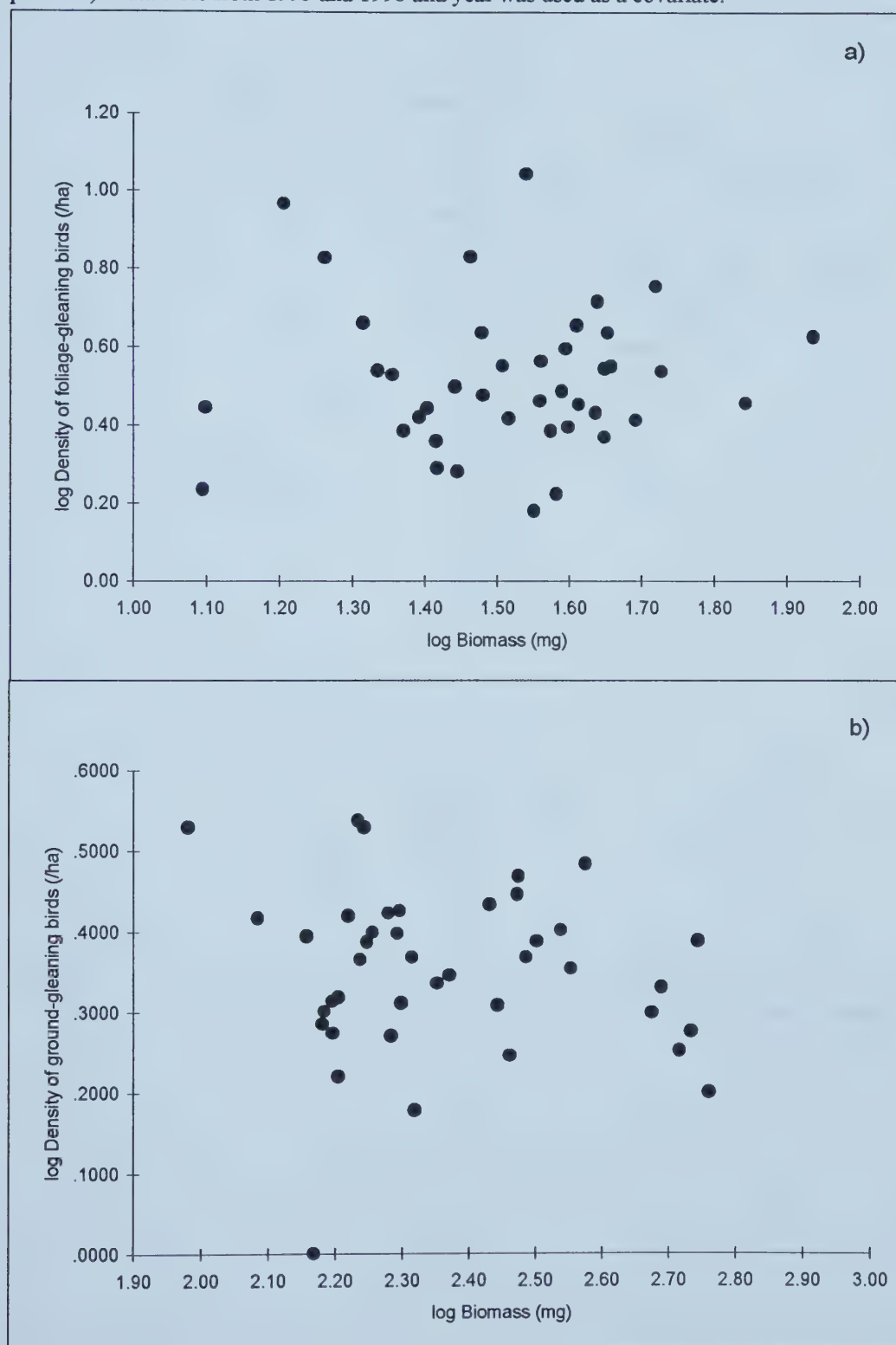
Figure 3.5 Biplots from redundancy analysis ordination of density of foliage-gleaning birds against vegetation characteristics and invertebrate biomass from sweep nets in (a) 1995 and (b) 1996. Invertebrate biomass was not as important as vegetation characteristics for predicting songbird density. See Appendix 2.3 for species codes.
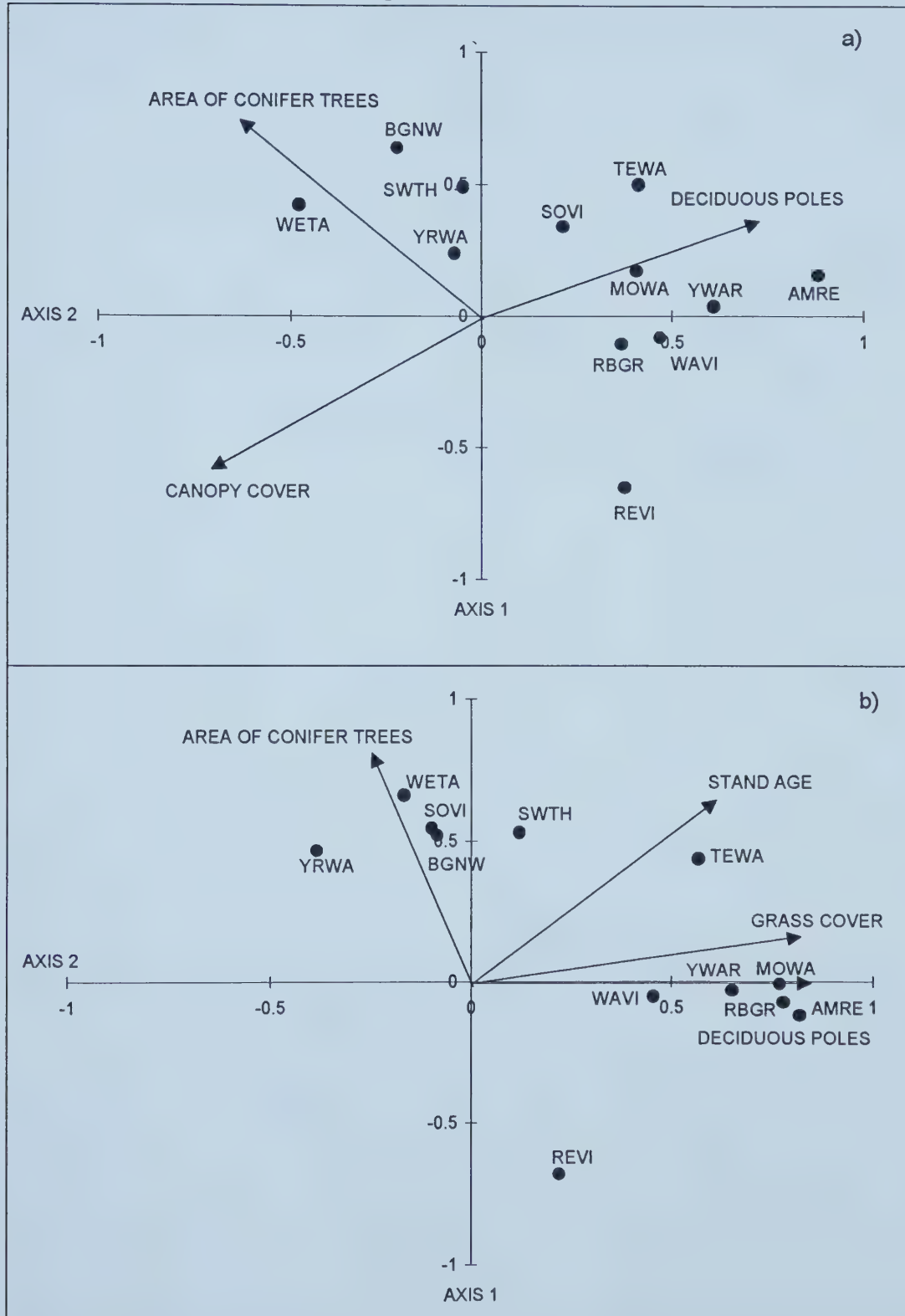
Figure 3.6 Biplots from redundancy analysis ordination of density of ground-gleaning birds against vegetation characteristics and invertebrate biomass from pitfall traps in (a) 1995 and (b) 1996. Invertebrates biomass was not as important as vegetation characteristics for predicting songbird density. See Appendix 2.3 for species codes.
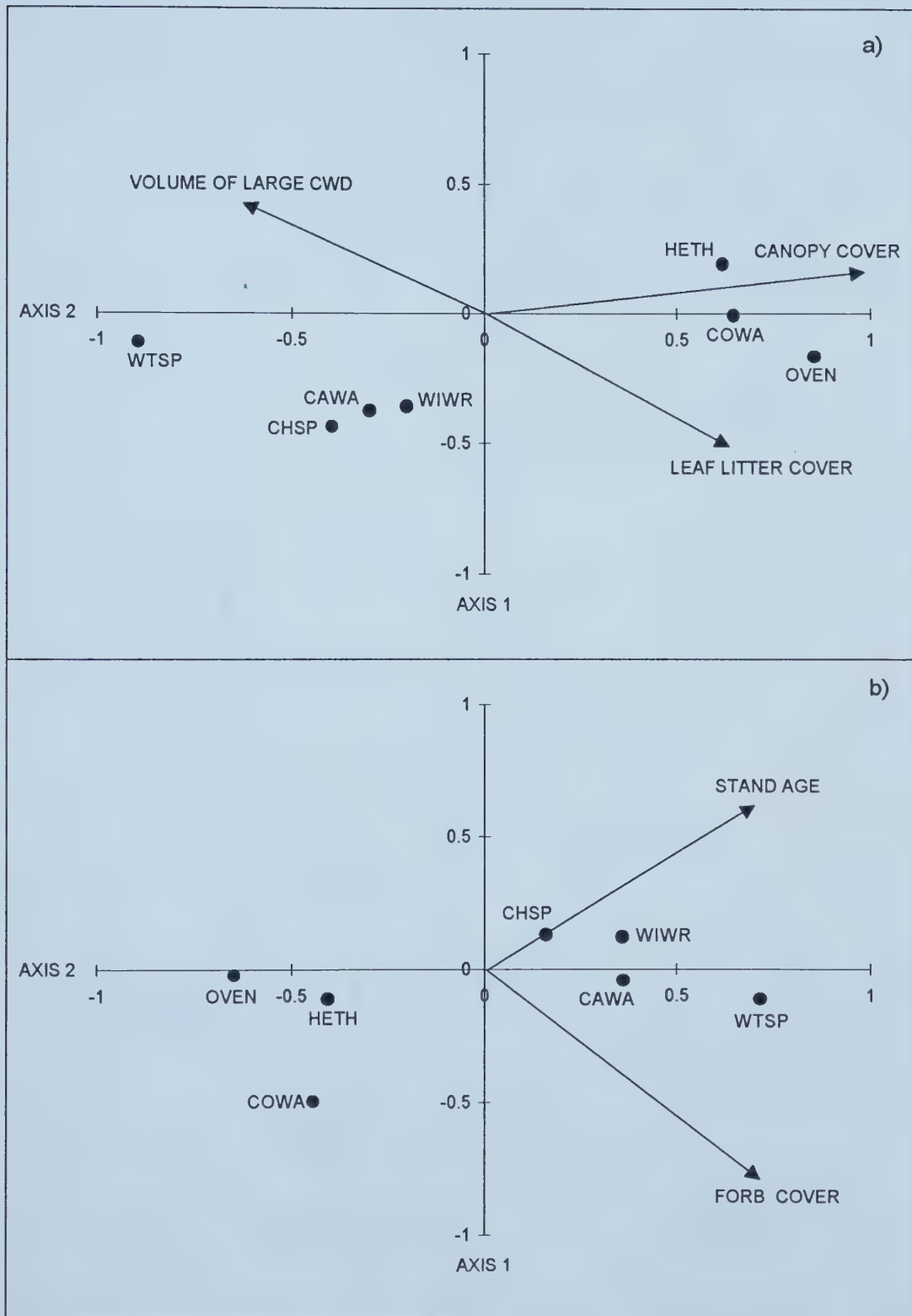
Figure 3.7. Biplots from redundancy analysis ordination of invertebrate biomass, as measured by sweep net sampling, and vegetation characteristics in (a) 1995 and (b) 1996.
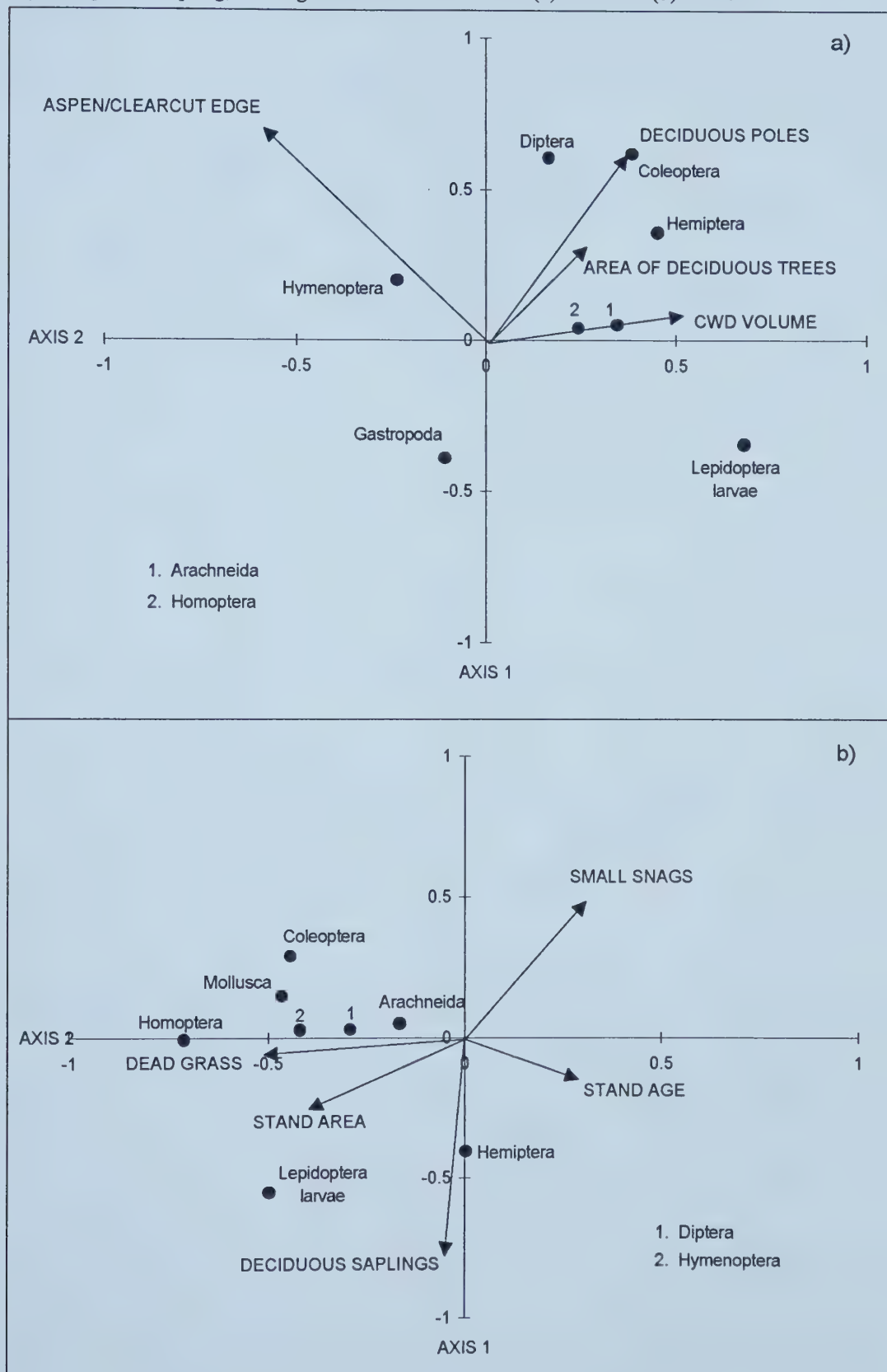
Figure 3.8. Biplots from redundancy analysis ordination of invertebrate biomass, as measured by pitfall trap sampling, and vegetation characteristics in (a) 1995 and (b) 1996.
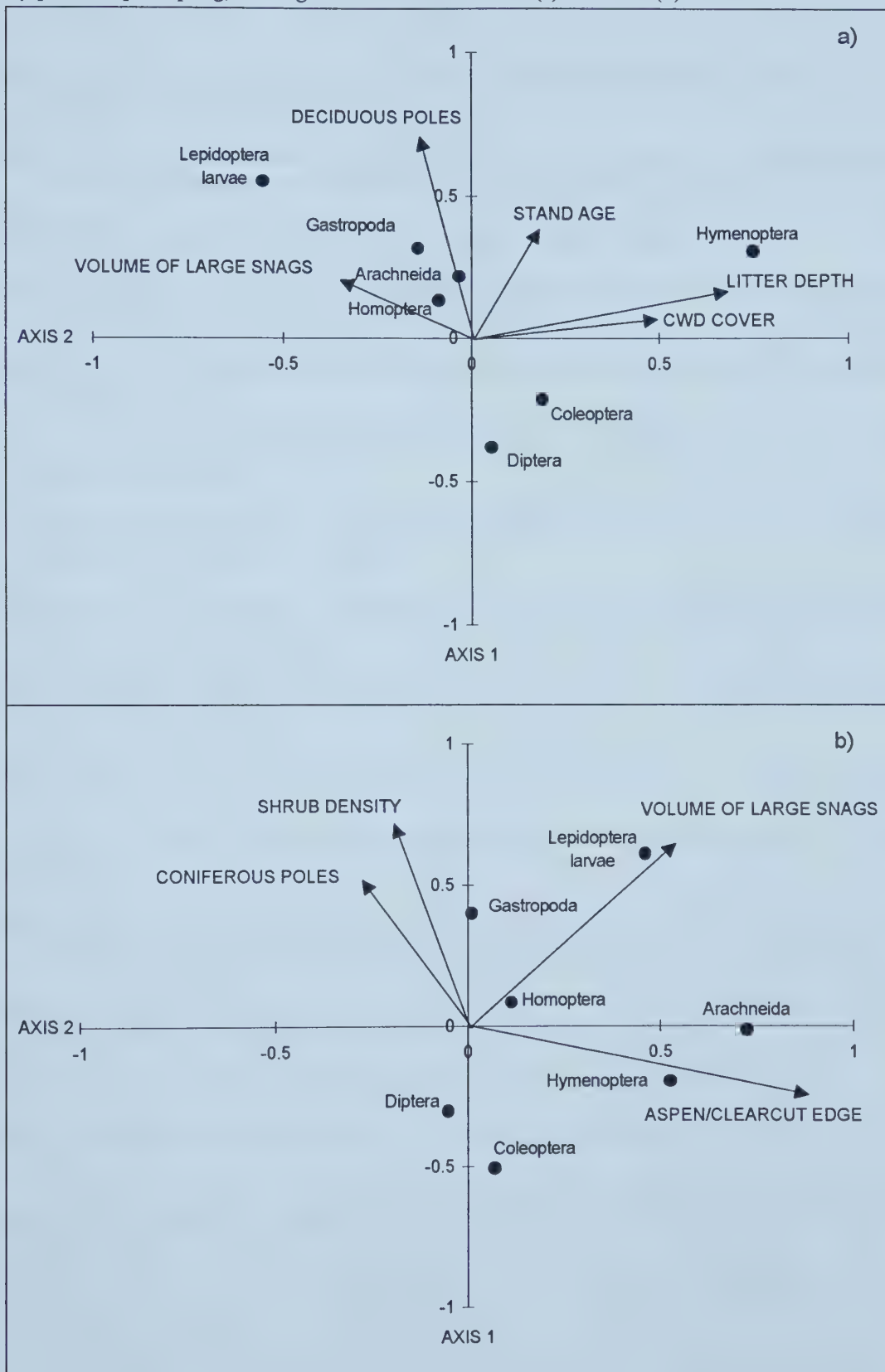
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Chapter 4: Predation in heterogeneous forests: a comparison at natural and anthropogenic edges.

4.0 Introduction

Songbirds nesting at forest edges can suffer higher rates of predation than those nesting in forest interiors (reviews in Paton 1995, Andrén 1995). Predation on eggs and nestlings is the primary source of mortality for neotropical migrant songbirds and can have a large effect on songbird productivity (Martin 1992b). Predation may increase at edges because (i) habitats adjacent to forest stands may act as a source of predators that penetrate across the forest edge; (ii) songbird densities may increase at the edge and predators may focus their search efforts here; and (iii) edges may act as travel corridors that facilitate predator movement (after Andrén 1995).

A negative effect of forest edge has not been found in all studies: agricultural landscapes tend to show higher predation at edges while forested landscapes often show little effect (Andrén 1995, Donovan *et al*. 1997, Hartley and Hunter 1998 but see King *et al*. 1996). Agricultural and forested landscapes may differ in songbird density, as well as species and abundance of predators, and these factors may influence edge effects. In relatively homogeneous forests, songbird density may increase at anthropogenic edges if there is an increase in understorey complexity at the edge (Johnston 1947, Strelke and Dickson 1980), and predators can be attracted by higher prey densities. However, in heterogeneous forests, increases in songbird densities at the edge, compared with the interior, may be less likely to occur because there may be little difference in vegetation structure at the edge (Noss 1991, Chapter 2). In agricultural areas, the matrix between the forest patches supports a more diverse and more abundant predator fauna than in forested areas (Andrén 1995, Darveau *et al*. 1997) and opportunistic predators feeding in the matrix are likely to encounter nests (e.g. Angelstam 1986,Vickery *et al*. 1992).

Many studies of nest predation have examined vegetation structure and composition around the nest but have neglected larger scales at the stand and landscape level. Predators operate at a variety of spatial scales and therefore, these same scales should influence foraging success (e.g. Pedlar *et al*. 1997). At the nest level, vegetation may influence the

probability of finding a nest for predators that use visual cues (Bowman and Harris 1980). In past studies, vegetation around the nest does not consistently affect the probability of predation (e.g. Rudnicky and Hunter 1993, Seitz and Zegers 1993, Howlett and Stutchbury 1996), probably because species and abundance of predators differ between areas. At larger scales, both stand and landscape composition may affect the probability of predator presence by influencing habitat selection and dispersal (e.g. Huhta 1995, Sykes 1996, Pedlar *et al.* 1997, Hannon and Cotterill 1998, King *et al.* 1998). Donovan *et al.* (1997) have shown that landscape scale analyses can be significant for predicting edge effects. In other heterogeneous systems, landscape composition has been an important determinant of species abundance (Orians and Wittenberger 1991, McGarigal and McComb 1995, Roland and Taylor 1997).

Edges in the boreal mixed-wood forest of northern Alberta have been created by both anthropogenic and natural processes. Anthropogenic edges have been made in old aspen stands through large-scale clearcut-logging practices and clearing for oil and gas exploration. Currently, 195 662 km² of forest has been leased to forestry companies in Alberta (D. Price, Alberta Environmental Protection, pers. comm.). Logging results in a checkerboard pattern of clearcuts and forest blocks. The oil and gas industry fells timber for gas wells, pipelines and seismic exploration lines. Within Alberta's forested regions, 14 000 km of seimic lines are cut per year, plus an additional 20 000 km of lines are re-shot (thus, re-cleared) (R. Jamieson, Alberta Envionmental Protection, pers. comm.). Natural edges in this system are formed by aspen and conifer stands that dominate the area due to a history of natural disturbance and variation in topography; edges are also formed by bogs, wetlands, lakes and rivers (Peterson and Peterson 1992).

Predation rates at edges in the boreal forest may vary with edge type and nest height. Differences in adjacent habitat should produce differences in predator abundance and species composition. Nest height may affect accessibility by predators. A study in this region by Cotterill (1996) showed that predation on eggs in shrub height nests was dominated by red squirrels (*Tamiascuirus hudsonicus*) and, to a very minor extent, by corvids such as gray jays (*Perisoreus canadensis*); ground nests were mainly preyed upon

by murid rodents, primarily, deermice (*Peromyscus maniculatus*) and red-backed voles (*Clethrionomys gapperi*). The majority of the diet of these animals is not composed of bird's eggs (Baker 1968, Rusch and Reeder 1978, Hansson 1985); instead these animals tend to prey opportunistically (Angelstam 1986). Predation events may be influenced predominantly by the productivity of adjacent habitat for predators. In the boreal forest, populations of red squirrels and gray jays are concentrated in conifer stands (Ouellet 1970, Rusch and Reeder 1978). Deermice are generalist foragers that exploit many habitats (Martell and Macaulay 1981, Martell 1983, Bayne and Hobson 1998) and, although red-back voles are thought to be more restricted to deciduous habitats (Martell 1981, Bondrup-Nielsen 1987), they are also successful in unscarified clearcuts (Weaver 1996). Finally, ease of predator movement throughout the landscape may influence predation rates (Andrén 1995). Predators may travel preferentially along seismic lines which are narrow, cleared paths (Bider 1968) and subsequently encounter nest adjacent to these routes.

Nest predation studies in forested landscapes are often limited because they are restricted to anthropogenic forest edges (e.g. Hawrot and Niemi 1996). The inclusion of natural edges in predation studies, particularly in heterogeneous landscapes, provides a broader context of the actual variation in predation rates that birds experience across their habitat (e.g. Weins 1995). In the boreal forest, natural edges may be a higher source of predation than anthropogenic edges because the clearings created by anthropogenic disturbance may be poor habitat for nest predators. I compared predation rates of artificial songbird nests at anthropogenic edges to both natural edges and the forest interior. I used both shrub and ground nests to estimate rates because just over 50% of territorial species of songbirds in these areas build nests at these heights (Song, unpubl. data). I also examined the role of vegetation at 3 scales: nest, stand, and landscape, in predicting predation events.

4.1 Methods

4.1.1 *Study site*

The study was conducted over 2 years (1995-96) in north-central Alberta, Canada, near Calling Lake (UTM Zone 12: 344214 E, 6133569 N) in boreal mixed-wood forest. Forested

areas are dominated by pyrogenic stands of trembling aspen, *Populus tremuloides,* balsam poplar, *Populus balsamifera*, and white spruce, *Picea glauca*, on upland sites (Strong 1992). Wetter sites are characterised by stands of black spruce, *Picea mariana* and willow, *Salix* spp. Major understorey species in aspen stands include: green alder, *Alnus crispa*, low-bush cranberry, *Viburnum edule*, prickly rose, *Rosa acicularis*, beaked hazelnut, *Corylus cornuta*, bracted honeysuckle, *Lonicera invulcrata*, and willow, *Salix* spp. Wild sarsaparilla, *Aralia nudicaulis*, dewberry, *Rubus pubescens*, fireweed, *Epilobium angustifolium*, bunchberry, *Cornus canadensis*, and various grasses are commonly found in the herb layer.

Sites were distributed over four contiguous 10 x 10 km townships. Clearcutting of aspen stands in a portion of this area was conducted in the winter of 1993 and summer of 1994. Clearcut blocks alternated with uncut blocks and averaged 25 ha in size. There is no large scale history of deciduous logging in this region (Strong 1992). No site preparation took place on the blocks after harvest. Conifer clearcutting was also conducted in this region in the winter of 1993, followed by blade scarification; these blocks were not included in this study. Seismic lines were cut in 1990 or earlier and were infrequently travelled by All Terrain Vehicles.

4.1.2 *Artificial nest study*

Predation was measured in old aspen (80-130 y) stands adjacent to: (1) white spruce stands; (2) clearcut aspen stands; (3) seismic lines; and, (4) in the interior of old aspen stands. Interior sites were a minimum of 200 m from a cutblock edge and 100 m from a seismic line. Area of aspen stands averaged 124.1 ± 21.5 ha and ranged from 15.5 to 392.6 ha. For each treatment, 250 m long transects were set parallel with the forest edge. Eight transects/treatment were established in 1995; an additional transect/treatment was added in 1996 for a total of 9 transects/treatment (Appendix 4.1). Nest stations were set at a random distance from the edge into the aspen stand, from 5 to 50 m away. Both a shrub and a ground nest, each baited with a single, fresh, Chinese painted quail (*Coturnix coturnix chinesis*) egg, were set within 10 m of the nest station. Nest stations were a minimum of 25

m apart and each transect had 10 ground nests and 10 shrub nests. Shrub nests consisted of wicker aviculture nests (Hagen), dipped in a thick mud mixture and lined with grasses and leaves. Ground nests were made by loosely weaving grasses together and were marked with a nail and a 2 cm^2 piece of flagging tape that was hidden by the egg. Nests were set out in early June for 3 weeks, in synchrony with the nesting of local songbird populations, and were checked once per week.

Loss or damage to the quail egg was recorded as a predation event. Eggs that received only scratches to the shell (i.e. colouring was removed but shell was not broken) were not classed as depredated because the amount of scratches was highly variable and it could not be accurately assessed whether or not this type of damage would lead to hatching failure in an actual songbird nest. Eggs where the shell was cracked but the albumin remained intact were counted as predation events: Maxson and Oring (1978) noted that this type of predation by mice lead to hatching failure in Spotted Sandpipers, *Actitis macularia*.

Artificial nests were used because they provided a relative rate of predator activity between treatments although results did not necessarily reflect actual nest predation rates . Results from studies can overestimate predation rates on real nests (Wilson *et al.* 1998) and may not sample all species of predators (Haskell 1995). However, with artificial nests, I controlled nest placement and exposure time and avoided the logistical hurdles associated with finding nests in dense habitat. Because human scent can affect the outcome of artificial nest studies (Whelan *et al.* 1994), rubber boots and gloves were used during handling of nests and eggs and natural materials were used as much as possible in construction of the nests.

4.1.3 *Vegetation data collection*

Vegetation was quantified around the nest site from early July to early August each year. At each nest site, percent overhead and lateral cover were visually estimated. I measured overhead cover by estimating the amount of understorey vegetation within a 0.5 m diameter circle over the nest. Similarly, lateral cover was estimated around the nest from approximately 0.5 m distance. Canopy cover was measured using a spherical densiometer.

At every second nest station, detailed vegetation data were collected using 0.04 ha circular vegetation plots and a protocol modified from the BBIRD program (Martin 1992a). Within each plot, the number, species and diameter at breast height (DBH) of trees and snags were recorded. Within a 0.008 ha nested sub-plot, number and species of saplings (DBH<2.5 cm) and poles (DBH 2.5-8 cm) were measured. Plots were divided into 4 quadrants, such that the dividing radii pointed towards, away, to the left and right of the edge. At the 5 m point along each radius, using a 1 m^2 quadrat, data were collected on: ground cover (% of all green, shrub, forb, coarse woody debris, grass, dead grass and moss cover), and shrubs (number and species). Along each radius, number, diameter, length and rot class of coarse woody debris (CWD) were recorded. At each plot, average canopy height was recorded using a clinometer.

Landscape level data were classified using 1:20 000 aerial photographs. Habitat patches were summarized by dominant overstorey vegetation into the following categories: (1) deciduous forest; (2) upland coniferous forest; (3) clearcut; (4) black spruce bog/wetland; (5) lakes and rivers. Patches were outlined by hand and then scanned into the computer programme, Aldus Photostyler 2.0, and edited. Landscapes were measured at 3 radii around the transects: 250 m, 450 m, 1000 m. These radii are estimates of a range of distances covered during off-territory foraging and mate searching forays by adults, and juvenile dispersal by the three major nest predators in forested areas: deer mice, red-backed vole and red squirrel (Stickel 1968, Larsen and Boutin 1994, J. Bowman unpubl. data). Transects were considered independent if the buffer within a radius category did not overlap. I had considerable overlap in my 1000 m buffer and did not analyse this category because sample sizes were very low. In the 450 m buffer category, I removed 12 and 13 sites in 1995 and 1996, respectively and in the 250 m buffer category, I removed 8 sites to ensure independence.

The total number of pixels composing each patch type was calculated using a computer programme, HISTO (J. Brzutowski, U. of Alberta). The total amount of deciduous/coniferous edge and deciduous/clearcut edges was computed by quantifying the

number of adjacent pixels of the respective habitat types composing the edge. Total length of seismic lines and roads was also measured.

4.1.4 *Statistical analysis*
4.1.4.1 *Effects of edge type and nest type on predation*

The effect of edge type, nest type (ground or shrub) and year on incidence of predation was investigated using nested logistic regression with a quasi-likelihood estimation, such that the effect of transect was nested within edge type. The quasi-likelihood function makes no assumptions as to the dispersion of errors *a priori* but provides an estimate of that dispersion while fitting the model (McCullagh and Nelder 1989). Edge type was entered as a categorical variable with the interior site as the reference category.

Regression analyses assume that sampling points are not spatially autocorrelated (Cliff and Ord 1981). Predation events may lack independence from a variety of sources, e.g. concentration of predator activity within an area, differences in edaphic or vegetation features among sites. Independence among nest sites was calculated by examining whether the presence of a depredated nest affected the probability of predation at adjacent nests. I compared the actual pattern of nest predation to a random distribution using a G-test. The random distribution was generated using a two-sample binomial equation based on the probability of a depredated nests having adjacent nest(s) also depredated (after Hannon and Cotterill 1998). Adjacency effects were minimal in shrub nest data collected in 1995 (range of G=4.40 to 5.90, p= 0.111 to 0.052, depending on trial) but were clearly present in 1996 data (range of G=8.88 to 18.4, p=0.012 to <0.001). Both years of ground nest data showed very low adjacency effects (1995: range of G=2.44 to 3.43, p=0.295 to 0.180; 1996: G=4.84, p=0.089). Spatial autocorrelation among data points results in an artificial increase of statistical power through an inflated number of degrees of freedom (Legendre 1993). Although I could not determine the exact amount of spatial autocorrelation among my points, as a conservative measure, I used a nested design with α at 0.05 (instead of 0.10 common to conservation studies e.g. Schmiegelow *et al.* 1997) within my logistic regression analyses.

4.1.4.2 *Effects of edge type on vegetation*

To help explain any effect of edge, I compared vegetation characteristics of transects between edge types to determine if there were differences in habitat associated with edge type. Vegetation variables were analysed using one-way ANOVA's and I used the same variables as I used in the nest-level logistic regression analysis. Because I had sample sizes to provide sufficient power, I set α to 0.05. Variables were log-transformed, or arcsine square root-transformed for percents, to ensure normality. I used averaged measurements from each transect. Scheffé's post-hoc tests were performed on significant relationships (Day and Quinn 1989).

4.1.4.3 *Effect of vegetation on predation*

A one-way ANOVA was used to compare differences in lateral and overhead cover around ground and shrub nests. The effect of habitat variables on the incidence of predation was analysed for shrub nests and ground nests separately because different predators were active at each nest type (Cotterill 1996). Cumulative predation rates after 3 weeks were used for these analyses. Separate analyses were performed for 1995 and 1996 data using vegetation data collected each year.

Vegetation characteristics measured at the nest level were entered into a nested logistic regression to determine the role of vegetation around the nest on the incidence of predation. Independent variables were log(x+1)-transformed when necessary. A principle components analysis (PCA) was performed to reduce the large number of vegetation variables but did not produce factors that explained sufficient variation. Instead, I reduced correlated variables to a single representative variable that was biologically relevant and satisfied the assumptions of no multicollinearity. Twenty-five variables were entered into the regression: edge type; transect nested within edge type; distance of the nest from the edge; basal area of: deciduous trees (trembling aspen + balsam poplar + white birch, *Betula papyrifera*), subcanopy height deciduous trees (green alder, *A. crispa* + river alder, *A. tenufolia* + saskatoon berry, *Amelanchier alnifolia* + willow, *Salix* spp. + pin cherry, *Prunus*

pensylvanica), and, coniferous trees (white spruce + balsam fir, *Abies balsamea* + black spruce + jack pine, *Pinus banksiana*); average canopy height; average canopy cover; number of snags <12 cm DBH; total volume of snags >12 cm DBH; density of: deciduous poles, deciduous saplings, conifer poles, and, conifer saplings; lateral and overhead cover at the nest; shrub density; % green ground cover, % shrub cover, % CWD cover; number of CWD <11 cm; and, volume of lightly- and heavily- rotted CWD>11 cm DBH.

For the stand level analysis, stepwise multiple regressions were used to examine the effects of vegetation along the entire transect on the percentage of nests depredated per transect. Percentages were arcsine square root transformed and vegetation variables were log (x+1)-transformed to ensure normality. Because working at the stand level decreased my sample size substantially, I was more concerned about Type II error, thus I increased alpha to 0.10. I reduced the number of vegetation variables entered into the model to decrease the possiblity of spurious results and also included stand area. The following variables were entered: edge type, canopy cover, canopy height, area of stand, basal area of deciduous trees, basal area of coniferous trees, density of both deciduous and coniferous saplings and poles, % green ground cover, % shrub cover, density of shrub stems, volume of snags, number of CWD pieces < 11 cm and > 11 cm DBH.

To determine if landscape level data could explain any additional variation in predation results, I used the residuals from the stand level analysis to perform a second set of stepwise multiple regressions. A PCA was generated for each radius for both 1995 and 1996 to reduce the highly correlated data set. Length of seismic lines and roads was not included in the PCA but added separately into the regression. From each PCA, 3 factors explained 80.3 - 85 % of the variation and are summarized in Table 4.1.

4.2 Results

4.2.1 *Effect of edge type, year and nest type on predation rate*

There was a significant effect of edge type, year and nest type on predation rate but there were also several significant interactions between these factors (Table 4.2). On shrub nests, predation in 1995 was higher on nests at aspen/seismic edges than the forest interior

(Figure 4.1a). In 1996, predation was higher on nests at aspen/white spruce edges than all other sites (Figure 4.1a). There was also significant variation in predation levels between transects: rates ranged from 0-80%. Predation rates dropped between years, from 32.8 ± 2.6% in 1995 to 18.9 ± 2.1% in 1996. On ground nests, there was no effect of edge type on predation in either year. The incidence of predation dropped in 1996 from an average of 20.3 ± 2.2% to 8.6 ± 1.5%.

4.2.2 *Vegetation at forest edges*

The interior of aspen stands and those next to the 3 types of edge were essentially similar (Table 4.3). Increases in conifer density at aspen/seismic line and aspen/white spruce edges are notable since every mature conifer is a potential cone source for squirrels; however, these differences were not statistically significant.

4.2.3 *Nest level vegetation and predation*

Overall, predation was significantly higher on shrub nests than ground nests in both years (1995: 32.8 ± 5.2% vs. 20.3 ± 2.5%; 1996: 18.9 ± 3.5% vs. 8.6 ± 2.2%). Lateral and overhead cover surrounding the nest were also significantly lower around shrub nests (lateral: $F=339.35$, $p<0.0001$; overhead: $F=78.66$, $p<0.0001$; Figure 4.2).

Some vegetation characteristics differed between depredated and intact nest sites but these factors were not consistent between years. For shrub nests in 1995, sites where nests were depredated had lower canopy cover ($\beta=-0.026$), lower canopy height ($\beta=-0.046$) and lower % green ground cover ($\beta=-0.039$) than intact nests while in 1996, sites where nests were depredated were closer to the stand edge ($\beta=-0.038$) and had a higher basal area of subcanopy height deciduous trees ($\beta=14.42$) (Table 4.4).

For ground nests in 1995, similar to the shrub nests, sites where nests were depredated had lower canopy cover ($\beta=-0.026$), lower canopy height ($\beta=-0.045$) and lower % green ground cover ($\beta=-0.039$) than intact nests (Table 4.4). In 1996, sites where nests were depredated were closer to the stand edge and had a higher density of conifer poles than intact nest sites (Table 4.4).

For all the nest level analyses, both the effect of edge and transect nested within edge are statistically significant (Table 4.4). For ground nests, these differences are unlikely to be biologically significant since differences between the interior and any edge type are maximum of 5-6% (vs. 15-29% differences for shrub nests).

4.2.4 *Stand level vegetation and predation*

Some vegetation characteristics predicted predation at the stand level but again, results were not consistent between years and the variation explained by the regression equations was very low. These stand level analyses did confirm my results from the logistic regression analysis on edge effects. For shrub nests in 1995, predation increased at aspen/seismic edges but no vegetation features predicted predation rates ($F=2.90$, $p=0.099$, $R^2=0.058$). In 1996, predation was higher in stands with decreasing basal area of conifer trees as well as at aspen/white spruce edges ($F=5.75$, $p=0.007$, $R^2=0.125$). For grounds nests in 1995, predation was higher in stands with less small CWD ($F=6.59$, $p=0.016$, $R^2=0.153$). In 1996, predation increased as stand area decreased and the basal area of conifer trees decreased ($F=5.32$, $p=0.0099$, $R^2=0.198$).

4.2.5 *Landscape level vegetation and predation*

Predation rates on shrub nests and on ground nests were not predicted by habitat features within the 250 m radii in either 1995 or 1996. The 450 m radii did explain some additional variation in predation rates for both nest types. On shrub nests in 1995, there was a significant inverse relationship between factor 3 and incidence of predation ($F=4.11$, $p=0.058$, $R^2=0.14$) such that predation tended to increase as the amount of conifer forest cover increased and the amount of deciduous forest cover decreased. In 1996, that relationship did not hold; there was a significant inverse relationship between factor 2 and incidence of predation ($F=5.57$, $p=0.028$, $R^2=0.17$). Here, predation tended to increase as the amount of bog/wetland and water cover increased and the amount of deciduous forest cover decreased. For ground nests in 1995, predation rates were positively and negatively related with factor 2 and factor 3, respectively ($F=3.52$, $p=0.049$, $R^2=18$). Predation rates

on ground nests increased as the amount of bog/wetlands and conifer cover increased and as the amount of deciduous cover decreased. In 1996, no factors predicted predation on ground nests in the 250 m buffer category.

4.2.6 *Predator identification*

Egg fate was categorised as: untouched, scratched, tap crack (shell cracked but albumin intact), peck hole, shell fragments or missing (Table 4.5). Scratched eggs were identified by Cotterill (1996) as evidence of activity by murid rodents. In 1995, 3 times as many ground nest eggs were scratched as were shrub nest eggs, which again suggests higher activity of murid rodents on ground nests. In 1996, equal percentages of ground and shrub eggs were scratched although overall numbers are lower. Peck holes, taken as evidence of avian activity, were very rare. Shell fragments, suspected evidence of red squirrel activity, were almost 4 times more prevalent in shrub than ground nests and twice as prevalent in 1996. A large number of eggs were missing in both shrub and ground nest categories. Red squirrels and corvids are able to remove eggs intact, as confirmed by nest camera studies in this area (S. J. Song unpubl. data, Cotterill 1996). Murid rodents are also capable of removing eggs intact: I found scratched eggs rolled away from ground nests. Maxson and Oring (1978) documented similar events.

4.3 Discussion

Predation in 1995 on shrub nests was higher at aspen/seismic line edges than in the forest interior. In 1996, predation rates remained similar at aspen/white spruce edges but dropped at aspen/seismic and aspen/clearcut edges. Patterns of red squirrel activity may explain these events. Red squirrels have historically been found in the highest densities in spruce habitats and lowest in aspen habitats (Rusch and Reeder 1978). White spruce is the best quality habitat for squirrels, likely due to the supply of their preferred food, white spruce cones (Kemp and Keith 1970). If squirrels prey opportunistically upon songbird eggs (Angelstam 1986), incidental predation events are more likely to occur near habitats that support squirrel populations and where squirrels are already foraging. Vickery *et al.*

(1992) note a similar phenomenon in grassland birds nesting near skunk foraging sites. By chance, densities of conifer trees at seismic sites were double that at interior and aspen/clearcut edges. If squirrels are the major nest predator, this may explain why they were more active here in 1995. Conifers were 3-4 times higher in aspen/white spruce sites than at interior or aspen/clearcut edges which would also increase the probability of squirrel presence. The decrease at aspen/seismic edges in 1996 can be explained by a change in squirrel numbers. Based on records from trappers who snared red squirrels consistently in both years, populations dropped in 1996 (e.g. 1995-1996: line 2795: 401-182 individuals; line 2420: 240-76 individuals; E. Powder, pers. comm., B. Treichel, Alberta Environmental Protection, Fish and Wildlife Branch, pers. comm.). At lower population levels, squirrels are less likely to disperse out of higher quality habitats, i.e. near white spruce stands, and may not be utilising small patches of conifer within aspen/seismic line sites (Kemp and Keith 1970). Corvids, another possible shrub nest predator, were not highly abundant in this region and population sizes did not change significantly between years (S.J. Hannon unpubl. data, S.J. Song unpubl. data).

No edge effect was evident on ground nest predation in either year. Weaver (1996) suggests that an edge effect on predation of ground nests at aspen/clearcut edges is not expected. In her study on deermice and red-backed voles conducted approximately 110 km ESE from my site, only male deermice increased in density at the forest edge. However, overall densities were very low (12 males/ha trapped over an entire summer). These results are confirmed by unpublished studies conducted in Calling Lake in 1994: deermice densities were similar in aspen stands and in clearcuts but densities were very low (<7 animals total) (A. Chan-McLeod, unpubl. data). Generally low densities of murid rodents in aspen stands may explain the low predation rates on these nests.

The lack of an edge effect on predation of both shrub and ground nests at aspen/clearcut edges concurs with Andren's (1995) conclusion that edge effects are often not apparent in forested landscapes. Clearcuts and aspen forests next to clearcuts probably do not provide a more favourable habitat than the forest interior or natural edges for the major nest predators in this ecosystem. In agricultural settings, predator populations are often supported by food

sources provided by human activity outside of the forest (Angelstam 1986, Andrén 1995)--this may not occur in young clearcuts. Aspen regenerates rapidly and densely by suckering: a closed canopy is achieved in just 3-4 years in most stands (Peterson and Peterson 1992). Further, human populations are low in the area. Both these factors help to limit invasion of species such as Black-billed Magpies, *Pica pica*, American Crows, *Corvus brachyrhynchos*, Blue Jays, *Cyanocitta cristata*, striped skunks, *Mephitis mephitis*, domestic cats and dogs that are important nest predators in areas of higher human activity (e.g. Hannon and Cotterill 1998).

Overall, I found that predation on shrub nests was higher than that on ground nests. Similar results were found by Yahner and Cypher (1987), Yahner and Scott (1988), Seitz and Zegers (1993) and also by Martin (1992b) in a review of nesting success of neotropical migrant passerines; but not by Best and Stauffer (1980), Loiselle and Hoppes (1983), Wilcove (1985), Bayne and Hobson (1997) nor, most notably, by Cotterill (1996) in the same region as my study. Cotterill's study differed in that she used plasticene eggs and quail eggs and classified scratched eggs as predation events. Plasticene eggs could attract predators (Cotterill 1996). Predation rates on ground and shrub nests are approximately equal in 1995 if scratched eggs are counted as predation events, but predation on shrub nests is still higher than on ground nests in 1996. Cotterill's study was conducted in 1993-94 and populations of murid rodents were probably at higher density during these years (ground nest predation ranged from 30% to 85% in aspen stands). The decline in ground nest predation from 1995-96 may be indicative of a crashing population of murid rodents. Further, shrub nests were made of wicker and were probably more visible versus ground nests made from grass. Cover around the ground nests was also higher. Finally, red squirrels and jays, if they are the main predators of shrub nests, are probably more effective predators because they are more successful at breaking shells and removing eggs than mice (Fenske-Crawford and Niemi 1997).

Vegetation features were not good predictors of predation in this system. Although analyses at the nest, stand and landscape level found some relationship between vegetation and predation, results were not consistent between years and relationships were not strong.

Higher amounts of conifer in aspen/seismic and aspen/white spruce sites points to an increased presence of red squirrels but only in the landscape level analysis and only in 1995 were higher areas of white spruce trees linked to higher predation. Conversely, stand level analyses showed an opposite effect in 1996 for both ground and shrub nests; after the effect of edge was acounted for, predation rate was negatively affected by the area of conifer trees. However, if conifer density was the major difference between my treatments, adding this variable into the stand level regression analysis may not explain any additional variation after entering edge type.

Past studies involving mammals, snakes and corvids as predators found no relationship between vegetation characteristics and predation for both real (Joern and Jackson 1983, Vickery *et al.* 1992, Hanski *et al.* 1996, Howlett and Stutchbury 1996) and artificial nests (Gottfried and Thompson 1978, O'Reilly and Hannon 1989, Seitz and Zegers 1993, Hannon and Cotterill 1998). Hanski *et al.* (1996) suggest that olfactory cues are more important than visual ones for mammalian predators. However, other studies on artificial nests where mammals were among the principal nest predators did find inverse relationships between foliage density and cover and predation rates (Rudnicky and Hunter 1993, Leimgruber *et al.* 1994, Vander haegen and DeGraaf 1996b). Bowman and Harris (1980) showed that mammals will use both visual and olfactory senses to find nests. Probability of predation is likely due to a combination of factors besides vegetation within the aspen stand itself. A number of different predators operating opportunistically and using different searching strategies makes predation difficult to predict.

The landscape matrix surrounding a stand had an inconsistent influence on predation rates. The effect of landscape composition (1) was evident only in the 450 m buffer category, (2) was different between years and, (3) explained a small amount of variation (an additional 14-18% on top of the stand level analysis). The majority of predators remain relatively close to their territory (Waser 1985, Larsen & Boutin 1994). In boreal mixed-wood forests, red squirrel territory sizes average 0.75 ha (J. Fisher, unpubl. data) while territories of murid rodents average 0.12-0.47 ha (Bondrup-Nielsen 1987, Weaver 1996). Therefore, smaller scale characteristics may be more important for predation by red squirrels

and murid rodents. Predator activity within a stand was not affected by factors such as the amount of harvested vs. unharvested habitat in the surrounding landscape. Features such as presence of conifer or bogs and wetlands were more important. Despite some timber loss, the landscape was predominantly forested in my study (about 8% of the landbase is harvested, B. Olsen, unpubl. data) and there may be few barriers to movement in and out of stands as has been demonstrated in agricultural landscapes (e.g. Mader 1984, Sykes 1996).

The high level of spatial and temporal variation found in this experiment emphasises the role of stochasticity within this system. The variation most likely reflects the activities of opportunistic predators that are not specifically focusing on eggs as a food source. The variation in my results between years also highlights the importance of continuing nest predation studies for more than one year. Most nest predation studies are limited to one year (e.g. Yahner and Cypher 1987, Ratti and Reese 1989, Seitz and Zegers 1993, Leimgruber *et al*. 1994, Marini *et al*. 1995, Vander Haegen and DeGraaf 1996a, Vander Haegen and DeGraaf 1996b, Fenske-Crawford and Niemi 1997). My conclusions would have been markedly different if this study had been discontinued after the first year.

Although anthropogenic activity is a source of habitat loss for songbirds in the boreal forest, it does not cause an increased rate of nest predation in the short term. Predation rates may not increase in the long term, either, if human activity is restricted to logging and seismic lines. Darveau *et al*. (1997) point out that human occupation in forests quickly results in the increase of generalist predators, such as American crows, that feed on refuse. In Alberta, seismic lines and logging roads are used by hunters, anglers, campers, scientists and for recreational ATV use. The current policy of aggressive development of forest and oil and gas industries in Alberta (Pratt and Urquhart 1994) with its attendant road-building and urbanisation certainly may result in changes to the predator communities and subsequent increases in nest predation rates.

Table 4.1: Factors generated from PCA on landscape level data. See appendix 4.2 for loadings.

Buffer width	Factors
450 m	1: Unharvested vs. harvested landscape • high loadings for conifer, coniferous/deciduous edge; low loadings for clearcut, clearcut/deciduous edge 2: Wetland/water vs. forested landscape • high loadings for water bodies, bog; low loadings for deciduous 3: Deciduous vs. coniferous landscape • high loadings for deciduous; low loadings for conifer
250 m	1: Unharvested vs. harvested landscape • high loadings for conifer, coniferous/deciduous edge; low loadings for clearcut, clearcut/deciduous edge 2: Wetland/water vs. forested landscape • high loadings for water bodies, bog; low loadings for deciduous 3: Wetland vs. water landscape • high loadings for water bodies; low loadings for bog

Table 4.2: Effect of edge type, year and nest type on predation of artificial nests as determined by nested logistic regression with quasi-likelihood method.

Term	df	Deviance	Residual df	Residual deviance	F	p
Null			1359	1352.74		
Edge type	3	9.65	1356	1343.08	3.01	0.029
Year	1	35.48	1355	1307.61	33.16	<0.001
Nest type	1	28.76	1354	1278.85	26.88	<0.001
Transect(Edge)	32	116.94	1322	1161.91	3.42	<0.001
Year*Nest type	1	0.75	1321	1161.17	0.70	0.403
Year*Edge type	3	7.90	1318	1153.27	2.16	0.061
Nest type*Edge type	3	9.18	1315	1144.08	2.86	0.036
Year*Nest type*Edge type	3	8.23	1312	1135.86	2.56	0.053

Table 4.3. Comparison of means of vegetation measures in aspen stands across edge types, based on measurements made in 0.04 ha circular plots.

	Interior	Clearcut	Seismic	White spruce	F	p
Basal area of trees (m²)						
Deciduous	0.8728	0.8546	0.8110	0.8580	0.167	0.918
Subcanopy spp.[1]	0.0139	0.0258	0.0090	0.0199	1.430	0.252
Coniferous	0.0327	0.0383	0.0787	0.1277	2.326	0.093
Canopy cover (%)	55.6	57.4	55.8	56.3	0.474	0.703
Canopy height (m)	24.8	25.8	25.4	26.8	0.931	0.437
Snags <12 cm DBH (#)	9.2	9.9	9.8	7.1	0.173	0.914
Large snag volume (m³)	1.48	1.54	1.28	1.05	0.363	0.780
Decid. sapling (#)	32.6	52.0	30.7	23.5	1.415	0.257
Decid. pole (#)	4.4	7.4	5.2	2.1a	2.392	0.087
Conif. sapling (#)	0.7	0.8	1.4	2.2	2.432	0.083
Conif. pole (#)	1.3	0.4	0.7	0.8	2.385	0.087
Shrub density (/m²)	6.0	4.3	5.4	6.0	0.900	0.452
Green ground cover (%)	68.2	67.4	70.1	70.7	0.451	0.718
Shrub cover (%)	31.5	35.3	32.8	36.1	0.623	0.605
CWD cover (%)	6.1	5.7	6.3	5.0	0.574	0.636
CWD 0-11 cm DBH (#)	114.7	115.9	113.8	119.4	0.240	0.866
CWD >11 cm, low rot (m³)	0.491	0.606	0.438	1.002	0.880	0.462
CWD >11 cm, high rot (m³)	0.580	0.849	0.723	0.677	0.384	0.765

1. Subcanopy species = deciduous trees that never were observed to reach canopy height. Included: *Alnus crispa, A. tenufolia, Amelanchier alnifolia, Salix* sp., *Prunus pensylvanica.*

Table 4.4: Nested logistic regression models relating the incidence of predation to vegetation characteristics around a nest site by year and nest type.

Nest type	Year	Term	df	Deviance	Residual df	Residual deviance	F	p
Shrub	1995	Null			319	405.02		
		Edge type	3	15.47	316	389.55	5.912	0.001
		Canopy cover	1	8.21	315	381.34	9.416	0.002
		Canopy height	1	4.90	314	376.44	5.614	0.018
		Green grd. cover	1	4.79	313	371.65	5.487	0.020
		Transect (Edge)	28	114.09	285	257.56	4.671	<0.001
Shrub	1996	Null			359	348.92		
		Edge type	3	16.63	356	332.29	6.746	<0.001
		Subcanopy trees	1	2.98	355	329.30	3.628	0.058
		Distance to edge	1	7.31	354	322.00	8.893	0.003
		Transect (Edge)	32	91.07	322	230.92	3.411	<0.001
Ground	1995	Null			319	405.02		
		Edge type	3	15.47	316	389.55	5.926	0.001
		Canopy cover	1	7.55	315	381.00	8.670	0.004
		Canopy height	1	4.69	314	377.32	5.386	0.021
		Green grd. cover	1	4.78	313	372.54	5.497	0.020
		Transect (Edge)	28	114.86	285	257.67	4.714	<0.001
Ground	1996	Null			359	348.92		
		Edge type	3	16.63	356	332.29	6.762	<0.001
		Conifer poles	1	3.92	355	328.37	4.777	0.030
		Distance to edge	1	6.53	354	321.94	7.96	0.005
		Transect (Edge)	32	96.20	322	225.63	3.667	<0.001

Table 4.5: Breakdown of egg fate by nest type and year. Numbers represent percentage of all eggs (320/nest type in 1995 and 360/nest type in 1996).

Egg fate	1995		1996	
	Shrub	Ground	Shrub	Ground
Scratched	6.6	20.0	10.0	10.6
Tap crack	3.8	1.2	0.3	0.3
Peck hole	1.2	0.3	0.3	0.6
Shell fragments	14.4	3.8	5.0	2.5
Missing	14.4	15.0	14.2	4.7
Untouched	59.6	59.7	70.2	81.3

Figure 4.1: Effect of edge type on the incidence of predation on artificial (a) ground and (b) shrub nests in 1995 and 1996.
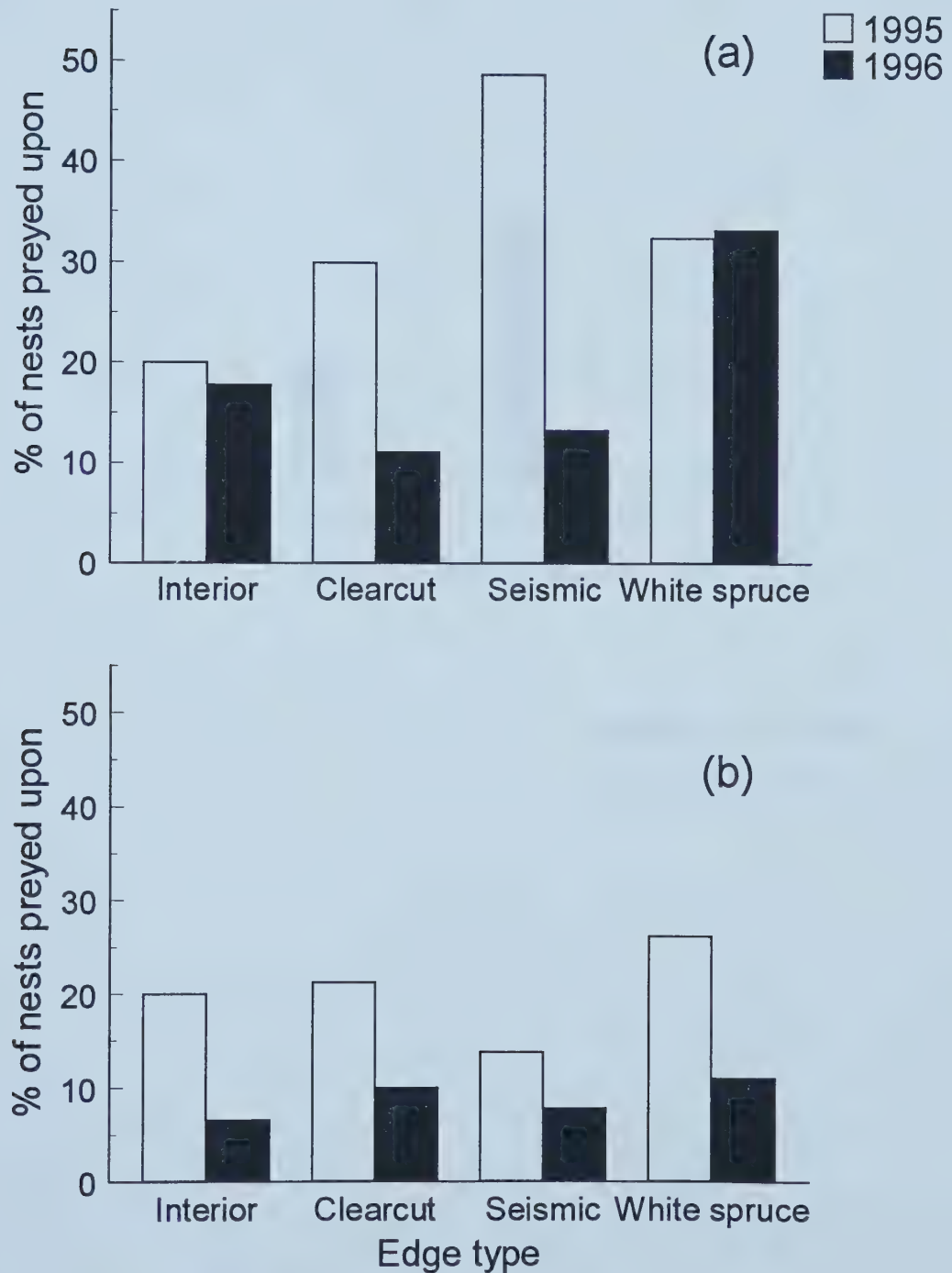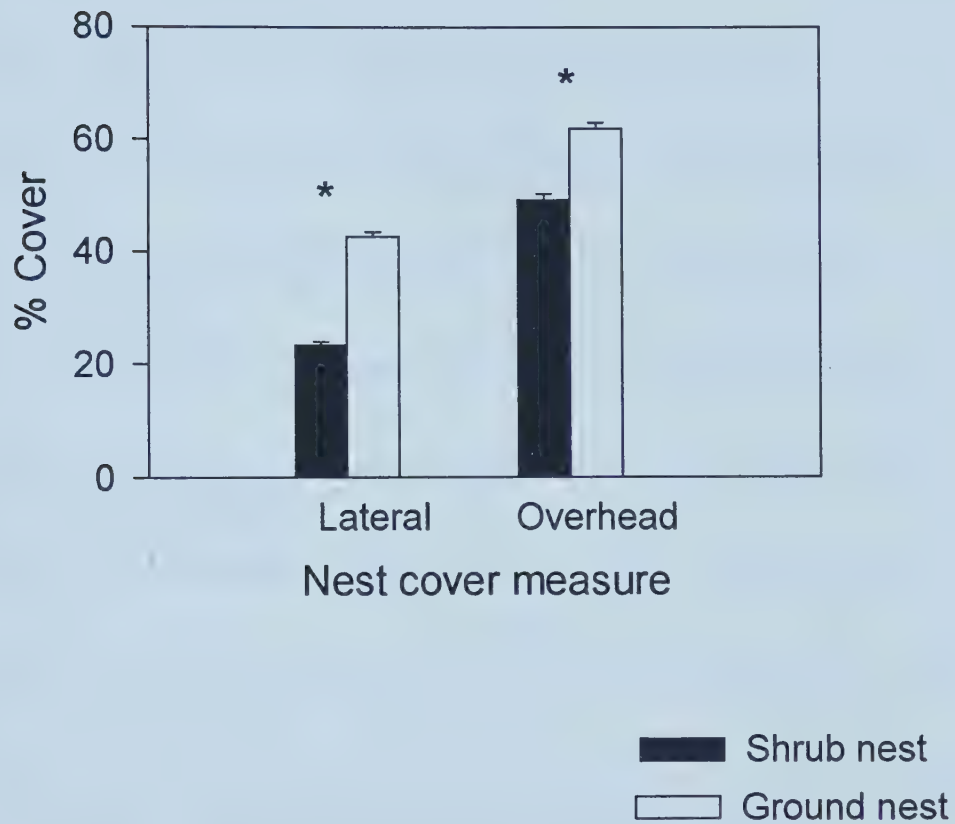
Figure 4.2: Comparison of nest cover over shrub and ground nests for both 1995 and 1996 combined. * denotes significant difference at p<0.05.

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Chapter 5: Conclusions and Management Implications

5.0 Summary of research findings and considerations for future research

Songbird communities did not differ in density or composition at different types of edge except for crowding observed at aspen/clearcut edges in the first year post-harvest. Density and composition of songbird communities were structured by vegetation characteristics that related to vertical and horizontal heterogeneity within an aspen stand e.g. understorey density, stand age, amount of conifer, and canopy cover.

Densities of some species were lower at aspen/white spruce edges than at aspen/clearcut edges and the forest interior. This was probably due to higher spruce content on the aspen side of this edge type. Aspen/clearcut edge was more of a habitat boundary for bird settlement than aspen/white spruce edge. Other than this, the effect of the abrupt aspen/clearcut edge did not differ from a graded aspen/white spruce edge with respect to species richness or overall densities. Species were not associated specifically with the edge or the interior, in contrast to other studies of forest edges created by clearings.

Biomass of invertebrates captured on foliage did not differ among edge types in either of the two years sampled. For invertebrates captured in pitfall traps in the first year post-cut, biomass was higher at aspen/clearcut edges than in the interior and biomass at aspen/white spruce was higher than at either of the two other sites. In the second year post-cut, biomass was higher at aspen/clearcut edges than at aspen/white spruce edges or the forest interior. Individual densities of invertebrate groups composing these samples varied in their response. Although songbird densities were not predicted by overall biomass of invertebrates, the density of individual species was related to biomass of individual invertebrate groups. However, the relationship between bird density and invertebrate biomass was not constant between years. Also, for the invertebrate group(s) that predicted a particular species density, its response to the forest edge did not necessarily reflect that bird's response to edge. Finally, although increasing understorey complexity or vertical

heterogeneity predicts increasing songbird densities, it did not consistently predict increasing invertebrate densities.

Predation on artificial nests was not higher at aspen/clearcut edges relative to other edges and to the forest interior for shrub or ground nests. In the first year post-cut, predation on shrub nests was higher at aspen/seismic line sites than all other sites, and in the second year post-cut, predation was higher at aspen/white spruce edges than at other sites. For ground nests, there was no difference in predation levels between sites although predation levels dropped overall between the first and second year post-cut. Shrub nests were probably depredated most frequently by red squirrels. Increased conifer availability coupled with changes in red squirrel numbers between years may explain results for shrub nests. Opportunistic predators, such as squirrels, are more likely to find nests where they are already foraging (e.g. Vickery *et al.* 1992) and red squirrels often forage on white spruce cones (Rusch and Reeder 1978). Ground nests were probably depredated mostly by microtines and predation levels on ground nests were generally low. The fate of an artificial nest does not reflect the fate of a real nest but artificial nests can provide a relative index of predation pressure (Wilcove 1985). Therefore, relative to the forest interior, aspen/seismic line and aspen/white spruce edges, songbird nests at aspen/clearcut edge are unlikely to experience higher predation rates.

Overall, aspen/clearcut edges did not act as an "ecological trap". Neither density of the songbird community nor predation events on artificial nests were higher here than in the forest interior or natural edges. In Gates and Gysel's (1978) work, they suggested that birds are "miscued" by vegetation structure at the edges of forests. Birds settled at the edge, responding to cues for adequate nest sites, cover, perches and forage and then suffered high predation because they had not yet adapted to anthropogenic edges, a recent phenomenon in evolutionary time. Some researchers have suggested that songbirds in the boreal forest may not experience negative edge effects at clearcut edges because disturbances such as fire create similar edges and birds have adapted to these conditions (Hunter 1992, Bayne and Hobson 1997). My results suggest that there is no selection pressure from increased predation at clearcut edges to force any adaptation specific to the

edge. In contrast, adaptation to aspen/white spruce edges may have occurred within some species. Predation on artificial shrub nests was high at aspen/white spruce edges, likely due to the presence of red squirrels. At this edge type, some species such as Red-eyed Vireo have lower densities than at other sites while other species such as Western Tanager are higher. Do Red-eyed Vireo's avoid white spruce to avoid predation? Do Western Tanagers have some behavioural adaptation (e.g. increased vigilance or defensive behaviour) to cope with increased predation pressure? A study of the behavioural ecology of these species would be an interesting avenue of future research.

At the outset of this study, almost no research on songbirds had been conducted in Canada's boreal forest (e.g. Welsh 1987) and no studies had looked at edge effects on birds in this region. Because so little was known about birds in the boreal forest, I adopted a community level approach to census the maximum number of species. Now that this groundwork has been laid and habitat associations are fairly well established for these species, a study on focal species to determine the effects of edge, predation and food supply on reproductive success would be extremely useful to confirm my results. Ultimately, recruitment should determine the impact of forest edge on songbirds. Intensive studies at the species level are also needed to establish the effect of edge on rare species. Species such as Blackburnian Warbler, Bay-breasted Warbler, Blackpoll Warbler or Black-and-White Warbler were rarely heard anywhere in my study area; an increased sample size would permit analysis of edge effects on these species.

A more detailed approach to invertebrate sampling may clear up some of the uncertainty as to whether I had observed true effects or whether results were artifacts of my methodology. A study that sampled directly on the territory and on confirmed foraging substrates, combined with observations of feeding behaviour would be extremely useful. In this study, I chose to maximize sampling effort and minimize my individual effort per animal. As a result I had fairly good sample sizes on invertebrate abundance and bird densities but little information on foraging behaviour. An intensive study would help to determine whether insect biomass reflects food availability for boreal songbirds.

Edge effects may occur in the future, and possibly only at mature (80 y) old stands and not older (120+ y) stands, based on my survey of vegetation at the edges aspen stands next to older (15 y) clearcuts. The number of deciduous saplings was higher in aspen stands next to older clearcuts than in the forest interior and this difference was more pronounced in mature aspen stands. Therefore, songbirds that are associated with increasing understorey complexity may increase at aspen/older clearcut edges while birds that avoid stands with heavy understorey may avoid these edges. A study that returned to these sites to monitor songbird response to aspen/older clearcut edges would serve to test my speculations.

Edges created by fire are another relevant edge with which to compare edges created by clearcutting. Using a natural disturbance regime as a potential model for timber harvesting is under investigation by researchers and forest companies (Hunter 1993, Bunnell 1995, Alberta Pacific Forest Industries Inc. 1997). Unfortunately, it was logistically impossible for me to include edges created by recent fires in my study. If vegetation has a similar dynamic at an edge created by timber harvesting as to an edge created by fire, I would expect that songbird communities would also respond similarly to those edges. However, if fires are followed by insect outbreaks (Amman and Ryan 1991), birds may increase at the edges of aspen stands next to new burns to take advantage of this food source (e.g. Hannson 1983). Although I did not detect a strong relationship between invertebrate biomass and density, perhaps larger differences in biomass between the edge and interior could have a strong effect on bird densities. Further, post-fire stands tend to have more structure than clearcut stands, especially snags (pers. obs.). Post-fire stands may act as less of a habitat boundary than clearcuts to birds in adjacent stands.

I chose to study the effect of edge on songbirds in the boreal forest primarily because songbirds were clearly sensitive to fragmentation in other landscapes (Whitcomb *et al.* 1981), they constitute the majority of vertebrate species in the boreal forest (Smith 1993) and many species are in decline in parts of their range (Sauer *et al.* 1997). Studying songbirds also has other logistic advantages--for example, they are diurnally active and relatively easy to census without the effort of trapping that is often necessary for other animals. Songbirds have also been suggested as biological indicators of forest condition

(Schmiegelow and Hannon 1993) but the absence of edge effects on songbirds at the community level does not guarantee that edges will not have negative effects on other systems. For example, many species of invertebrates and plants may be more sensitive than birds to differences in microclimate between the forest edge and the interior. Birds may not be the best biological indicators for the boreal forest because, generally, they have not shown a similar sensitivity to fragmentation as has been shown in eastern North America (e.g. Schmiegelow *et al*. 1997, Lambert 1998, this study). Because so little is known about ecological relationships in the boreal forest (Spence *et al*. 1997), we should be careful not to ignore the potential impacts of creating forest edge on other species. Indeed, it was this type of narrow attitude in the past, where the creation of edge was encouraged to improve conditions for game species, that inadvertently exacerbated the decline of songbirds.

5.1 Implications for management of the boreal mixed-wood forest of Alberta

5.1.1 *Is the creation of edge cause for concern?*

Current operating ground rules for deciduous timber harvest in Alberta state that an average cutblock should not exceed 40 ha in size and should be designed with irregular boundaries (Alberta Environmental Protection 1993). Cutblocks are also designed to limit "line of sight" to 400 m; therefore, cutblocks are often created with zig-zagging boundaries to limit the ability of hunters to view game from a long distance. Cutblocks are cut in a 2 or 3 pass system that results in an alternating pattern of cut and uncut blocks. Timber harvest that follows these regulations results in the creation of large amounts of forest/clearcut edge. My research provides no evidence that the creation of forest/clearcut edge affects density or structure of songbird communities except in the first year post-cut, where there may be some crowding effects as birds are displaced from habitats lost to clearcutting. Hagan *et al*. (1996) demonstrated that crowding can affect pairing success. However, crowding effects were ameliorated after one year in my study and the impact of lowered pairing success in a single season may or may not affect long term success. Three major caveats should be addressed before forest edge is dismissed as a conservation concern for

songbirds breeding in the boreal forest. Firstly, research on reproductive success should be conducted to confirm my results. Secondly, larger sample sizes of rare species are needed to determine their response to edge. Thirdly, long term research is needed to ascertain the effects of edge over time (e.g. is there real recovery from crowding effects?).

5.1.2 *Maintenance of variation in stand age and stand composition*

Maintaining the current range of stand age and stand composition within the boreal forest may be a more important focus than forest edge for timber planners. Older stands (120 + y) are distinct from mature stands (80+ y) because they have different bird and invertebrate faunas and different vegetation structure (Chapter 2, Lee *et al*. 1995, Schieck and Neitfeld 1995, Spence *et al*. 1997). Short rotation lengths that attenuate the distribution of stand ages such that older stands are largely removed from the landscape will also remove a large source of biodiversity in the boreal forest.

The presence of conifer can affect the composition of songbird communities as well as invertebrate biomass and the probability of predator presence. The patches of white spruce and aspen that compose the majority of the forested land base in the boreal region are not discrete units. There is a grading from pure aspen through mixed-wood through pure white spruce; composition and density of songbird communities will reflect these changes. Operating guidelines for aspen harvest require the reforestation of harvested conifer (Alberta Environmental Protection 1993). If the forest industry is committed to "maintain(ing) viable populations of all indigenous wildlife species, with good geographic distribution throughout the Forestry Management Agreement", as stated in the operating ground rules for Alberta Pacific Forest Industries Inc. (Alberta Environmental Protection 1993), careful consideration should be given to the configuration of deciduous and coniferous trees during reforestation efforts so that the natural variation of stand composition will be maintained throughout the boreal forest.

5.2 Songbirds in the future forest

The government of Alberta has embarked on a course of rapid exploitation of the boreal forest, through agriculture and oil, gas and timber extraction, with little commitment towards habitat protection (Pratt and Urquhart 1994, Schneider 1997, Nikiforik 1998, Timoney 1998). We have little idea how the cumulative effects of this activity will affect ecological processes in the boreal forest. My research, in conjunction with other research on songbirds in the region, suggests that fragmentation may have a less serious impact on songbirds than has been observed in eastern North America (Cotterill 1996, Machtans *et al.* 1996, Schmiegelow *et al.* 1997, Lambert 1998); however, the boreal landscape is still predominantly forested. Habitat loss, particularly loss of older aspen and mixed-wood stands, may be a more important consideration for many species. Although there have been indications of some commitment to maintain older age stands of aspen on the landscape (K. Reimer, Alberta Pacific Forest Industries Inc., pers. comm.), no clear plans about the configuration of these stands across the landscape have been made. If older stands are relegated to riparian buffer strips, they are unlikely to provide sufficient habitat to maintain songbirds, and possibly other species, associated with older stands (Hannon, unpubl. data).

Adaptive management, which takes an experimental approach to forest management and provides flexibility to change management practices as new technology and research develops, is a potential management solution. The government of Alberta, as well as various stakeholders within the boreal forest, have committed to the idea of adaptive management through agreements such as the Alberta Forest Conservation Strategy and the Alberta Forest Legacy (Alberta Environmental Protection 1997a, 1997b). One of the key components of adaptive management is to establish "control" or "benchmark" areas of wilderness that can be used as a basis for comparison for more intensively managed areas. Although the government has contributed funding towards research in the boreal forest, activity towards establishing protected benchmark areas has been virtually non-existent (Schneider 1997, Nikiforuk 1998, Marck 1998, Mitchell 1998). As a province, our attempt

at adaptive management will surely fail without this component and pressure should be maintained on our government to live up to its commitments.

Research is a vital component of an adaptive management approach, both for developing an appropriate design for benchmark areas and continuing to investigate ecologically-sound management strategies for industrial forests. One of the main challenges, as exemplified by this research, will be drawing conclusions about patterns and processes in the boreal forest when they have an inherently high degree of variability. Part of the problem with quantifying this variability is the small temporal and spatial scale of studies such as mine. Short term projects do answer some important questions and set the stage for the direction of future research. Ultimately, projects such as this one will contribute the most knowledge if they are part of a coordinated series of projects that are working towards long-term research goals. Until we have results from long term research, however, management strategies should be conservative to adequately maintain the boreal ecosystem in Alberta.

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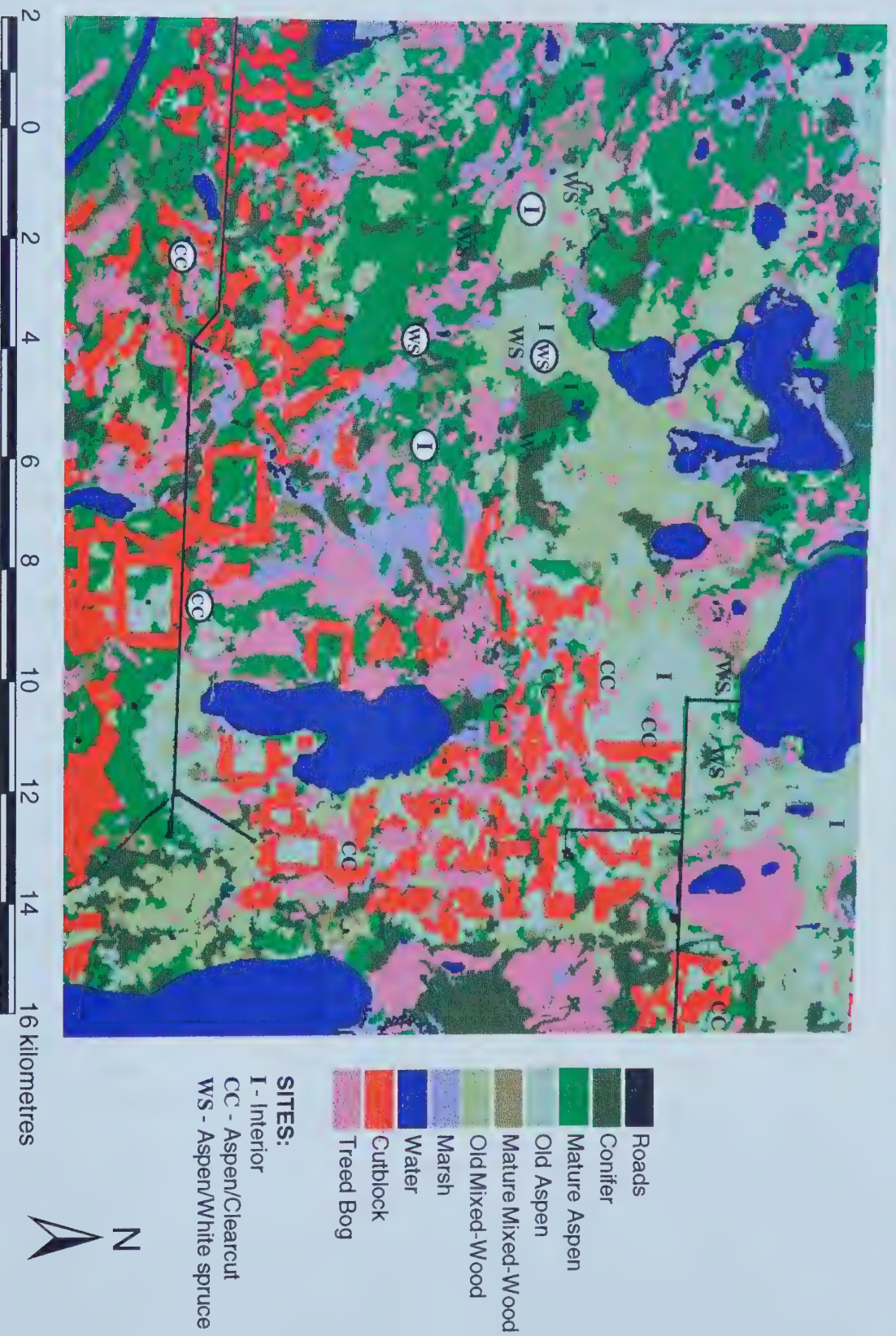
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Appendices

Appendix 2.1. Layout of a typical spotmapping grid. Grid was set parallel to edge for 250 m and extended in aspen for 150 m and into adjacent habitat for 50 m. Surveyers walked along the edge, along perpendicular boundaries and along a path set 100 m away from the edge into the aspen (dotted line).

EDGE

Adjacent Habitat

Aspen

50 m

100 m

50 m

200 m

250 m

⬤ 0.04 ha vegetation plot
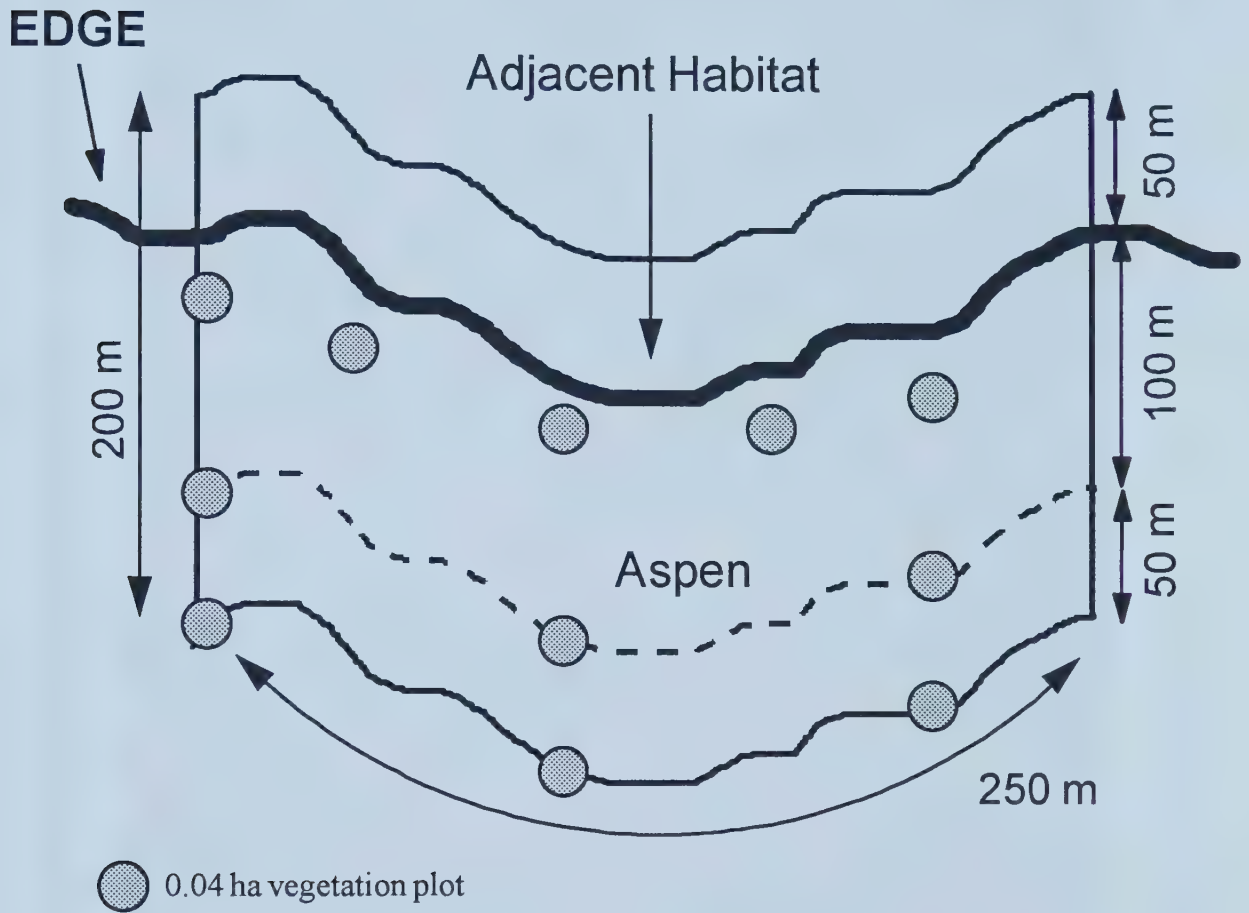
Appendix 2.2 Layout of spotmapping grids for censusing territorial songbirds. Circled sites were added in 1996.

SITES:
I - Interior
CC - Aspen/Clearcut
WS - Aspen/White spruce

Roads
Conifer
Mature Aspen
Mature Mixed-Wood
Old Aspen
Old Mixed-Wood
Marsh
Water
Cutblock
Treed Bog

N

16 kilometres

Appendix 2.3: List of territorial species recorded in old aspen stands in 1995-6 and their classification by migratory, nesting and foraging guilds.

Common name	Scientific name	AOU code	Migration[2]	Nesting[3]	Foraging[4]
Yellow-bellied Sapsucker	*Sphyrapicus varius*	YBSA	SDM	C	B
Western Wood-Peewee	*Contopus sordidulus*	WWPW	NTM	S	H
Least Flycatcher	*Empidonax minimus*	LEFL	NTM	S	H
Black-capped Chickadee	*Poecile atricapillus*	BCCH	R	C	F
Red-breasted Nuthatch	*Sitta canadensis*	RBNU	R	C	B
Winter Wren	*Troglodytes troglodytes*	WIWR	SDM	C	G
Golden-crowned Kinglet	*Regulus satrapa*	GCKI	SDM	S	F
Ruby-crowned Kinglet	*Regulus calendula*	RCKI	SDM	S	F
Swainson's Thrush	*Catharus ustulatus*	SWTH	NTM	S	F
Hermit Thrush	*Catharus guttatus*	HETH	SDM	G	G
American Robin	*Turdus migratorius*	AMRO	SDM	S	G
Solitary Vireo	*Vireo solitarius*	SOVI	NTM	S	F
Warbling Vireo	*Vireo gilvus*	WAVI	NTM	S	F
Red-eyed Vireo	*Vireo olivacus*	REVI	NTM	S	F
Tennessee Warbler	*Vermivora peregrina*	TEWA	NTM	G	F
Yellow Warbler	*Dendroica petechia*	YWAR	NTM	S	F
Magnolia Warbler	*Dendroica magnolia*	MNWA	NTM	S	B
Yellow-rumped Warbler	*Dendroica coronata*	YRWA	NTM	S	F
Black-throated Green Warbler	*Dendroica virens*	BGNW	NTM	S	F
Blackburnian Warbler	*Dendroica fusca*	BLWA	NTM	S	F
Bay-breasted Warbler	*Dendroica castanea*	BBWA	NTM	S	F
Black-and-white Warbler	*Mniotilta varia*	BAWW	NTM	G	B
American Redstart	*Setophaga ruticilla*	AMRE	NTM	S	F
Ovenbird	*Seiurus aurocapillus*	OVEN	NTM	G	G
Connecticut Warbler	*Oporornis agilis*	COWA	NTM	G	G
Mourning Warbler	*Oporornis philadelphia*	MOWA	NTM	G	F
Common Yellowthroat	*Geothlypis trichas*	COYE	NTM	S	F
Canada Warbler	*Wilsonia candensis*	CAWA	NTM	G	G
Western Tanager	*Piranga ludoviciana*	WETA	NTM	S	F
Rose-breasted Grosbeak	*Pheucticus ludoviciana*	RBGR	NTM	S	F
Chipping Sparrow	*Spizella passerina*	CHSP	NTM	S	G
White-throated Sparrow	*Zonotrichia albicollis*	WTSP	SDM	G	G
Dark-eyed Junco	*Junco hyemalis*	DEJU	SDM	G	G

1. Guild classification obtained from Ehrlich *et al*. 1988, Sauer *et al*. 1997.
2. Migratory classes: NTM, neotropical migrant, SDM, short distance migrant, R, resident.
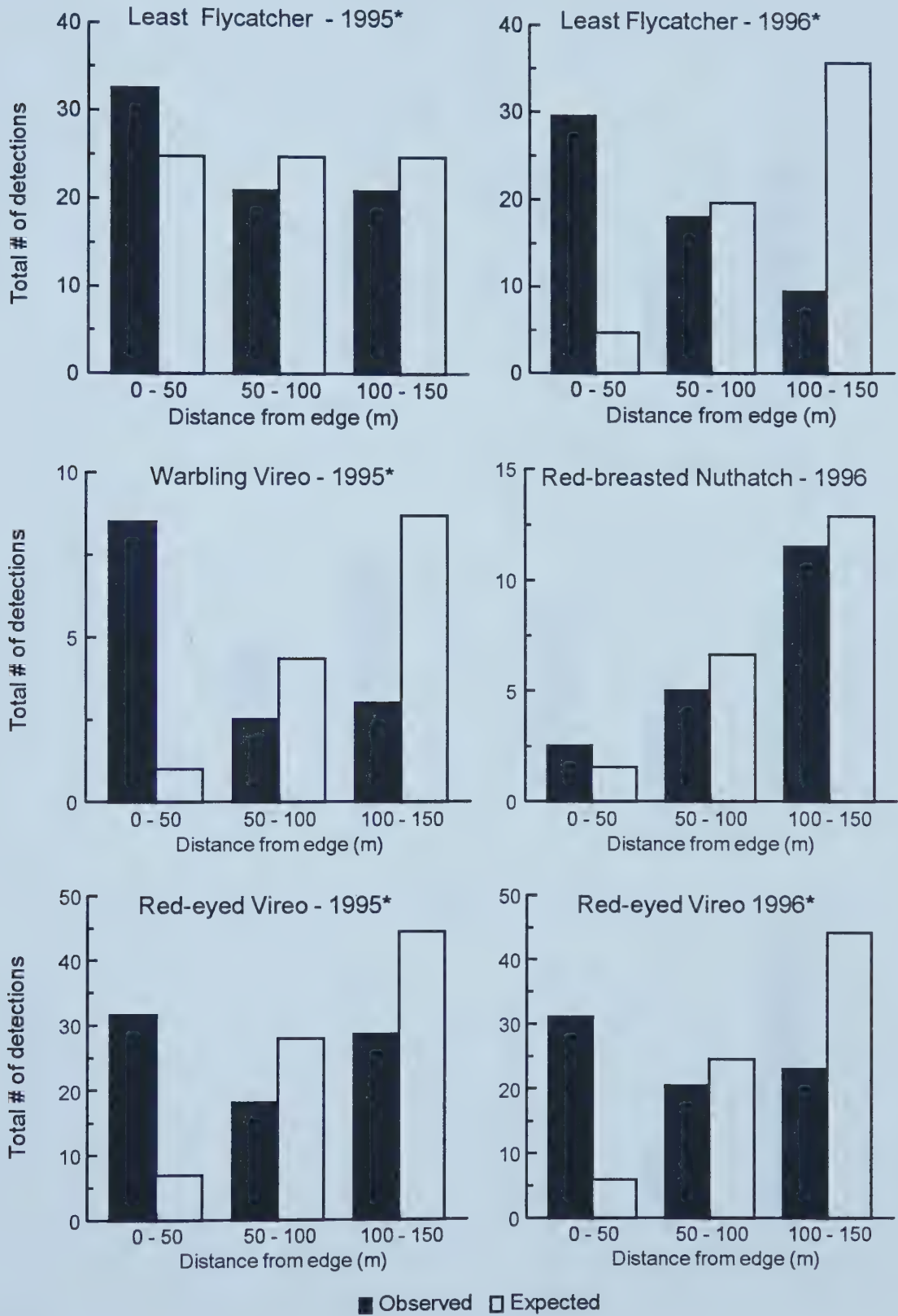3. Nesting classes: C, cavity nest, G, ground or low nest, S, shrub to canopy nest.
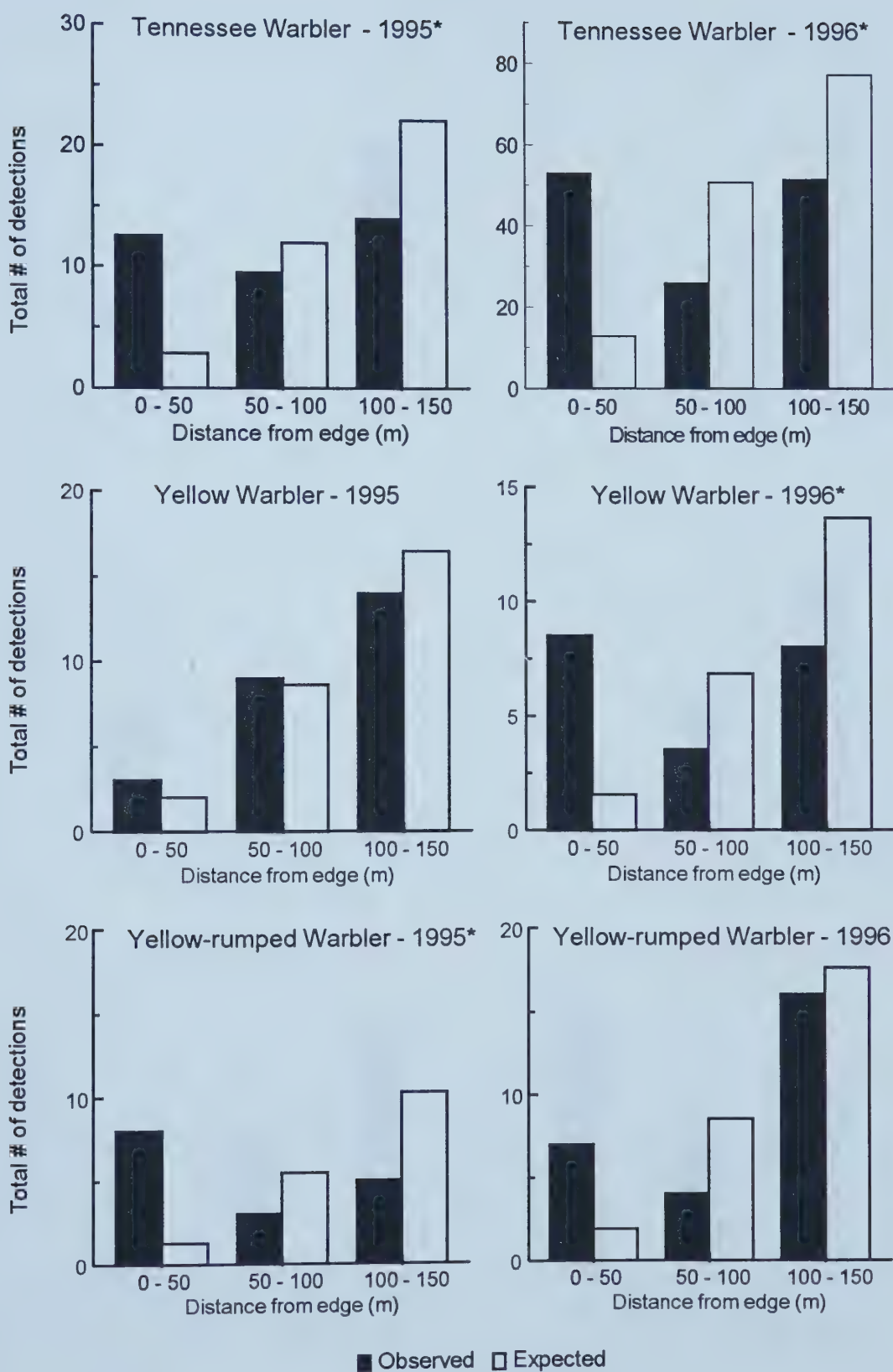4. Foraging classes: B, bark gleaner, F, foliage gleaner, G, ground gleaner, H, hawks.

Appendix 2.4. Common and scientific names and AOU codes of other bird species holding territories in study grids.

Common name	Scientific name	AOU code
Alder flycatcher	*Empidonax alnorum*	ALFL
Tree Swallow	*Tachycinete bicolor*	TRSW
Common Yellowthroat	*Geothlypis trichas*	COYE
Clay-coloured Sparrow	*Spizella pallida*	CCSP
Lincoln's Sparrow	*Melospiza lincolnii*	LISP
Swamp Sparrow	*Melospiza georgiana*	SWSP

Appendix 2.5. Distribution of total observed and expected detections of species at aspen/clearcut edges. * indicates significance at p<0.10.
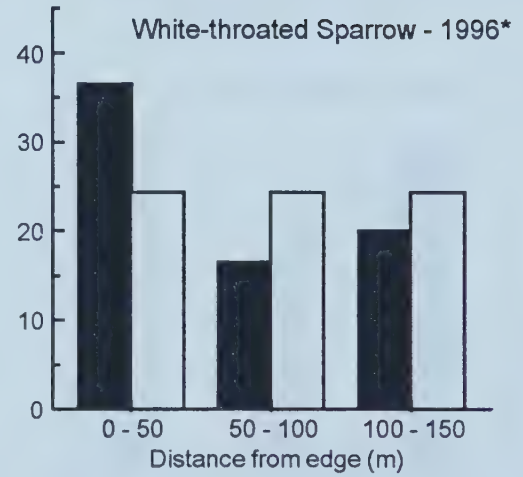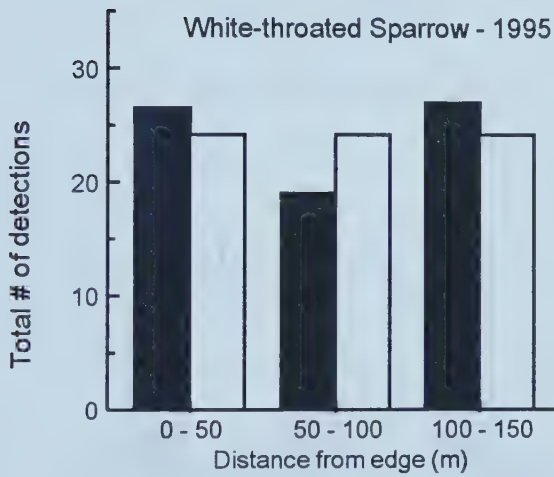
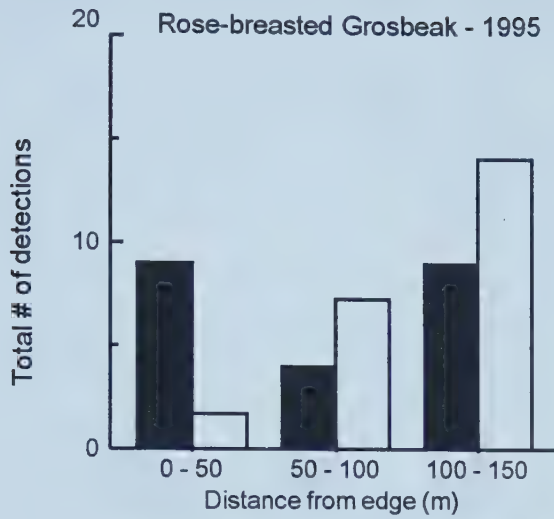Appendix 2.5. continued.

Tennessee Warbler - 1995*

Tennessee Warbler - 1996*

Yellow Warbler - 1995

Yellow Warbler - 1996*

Yellow-rumped Warbler - 1995*

Yellow-rumped Warbler - 1996

■ Observed □ Expected

Appendix 2.5. continued.

American Redstart - 1995*

American Redstart - 1996*

Ovenbird - 1995*

Ovenbird - 1996

Mourning Warbler- 1995*

Mourning Warbler - 1996*

Distance from edge (m)

Total # of detections

■ Observed ☐ Expected

Appendix 2.5. continued.

Rose-breasted Grosbeak - 1995

White-throated Sparrow - 1995
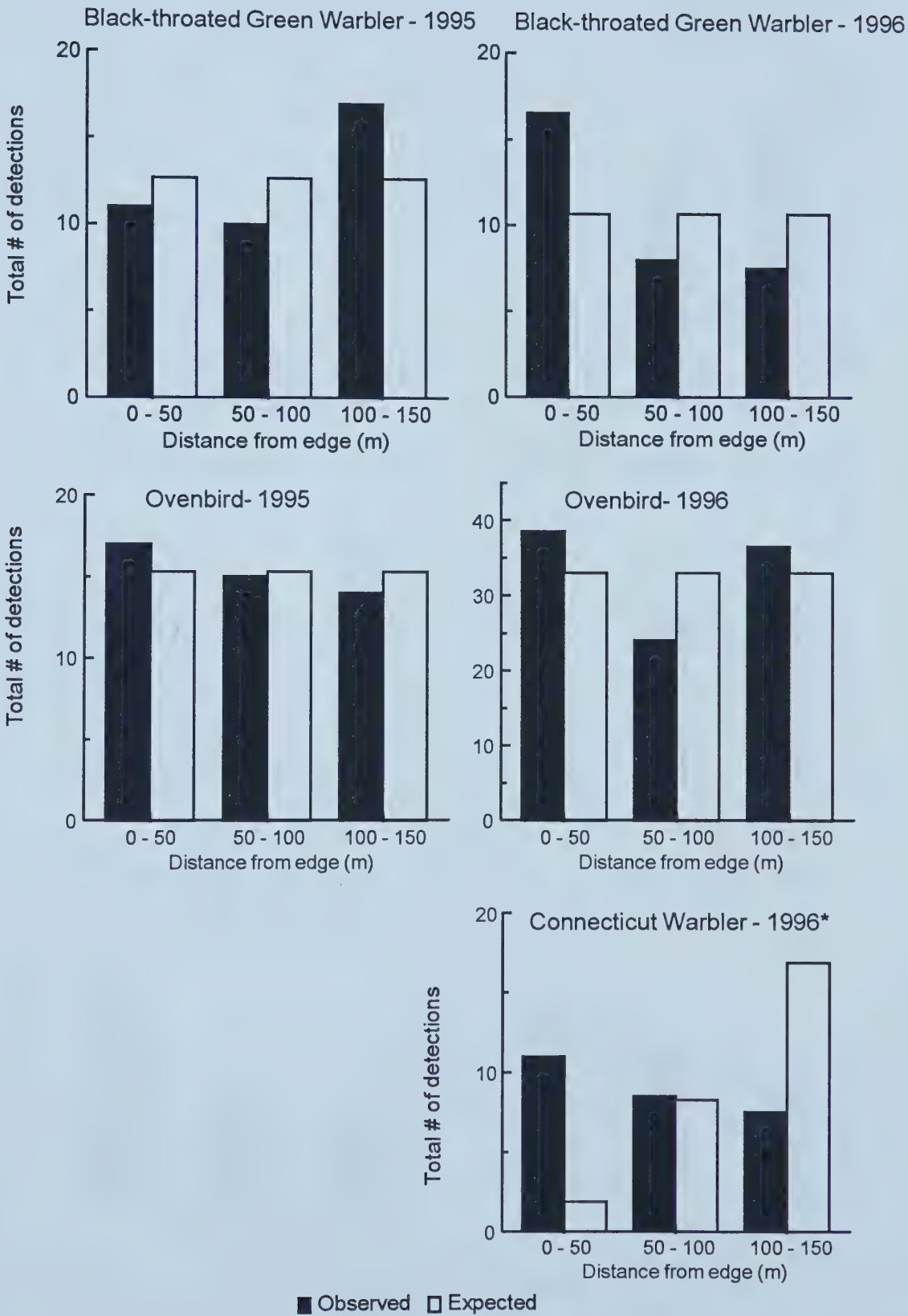
White-throated Sparrow - 1996*

■ Observed □ Expected
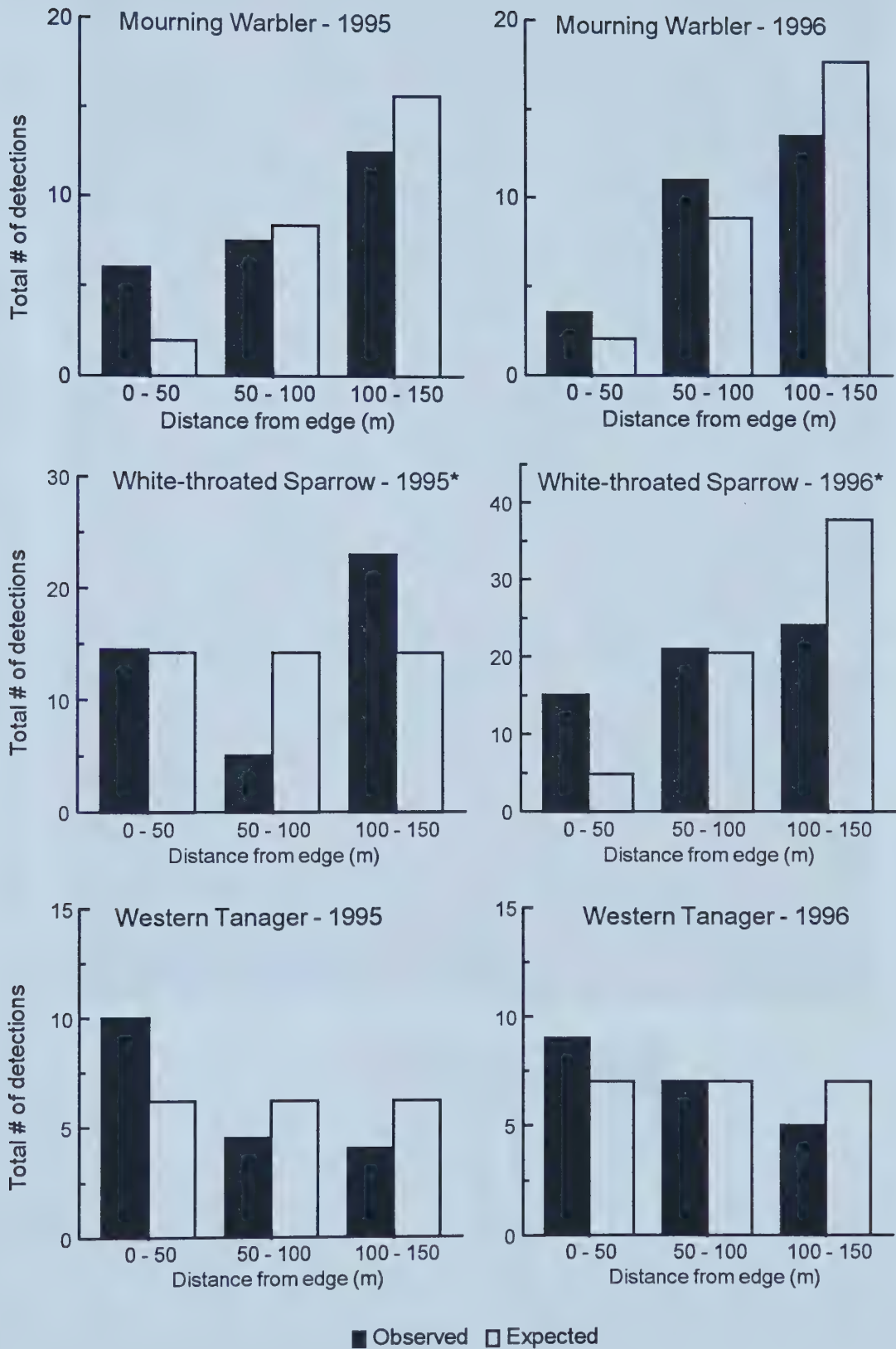
Appendix 2.6. Distribution of total observed and expected detections of species at aspen/white spruce edges. * indicates significance at p<0.10.
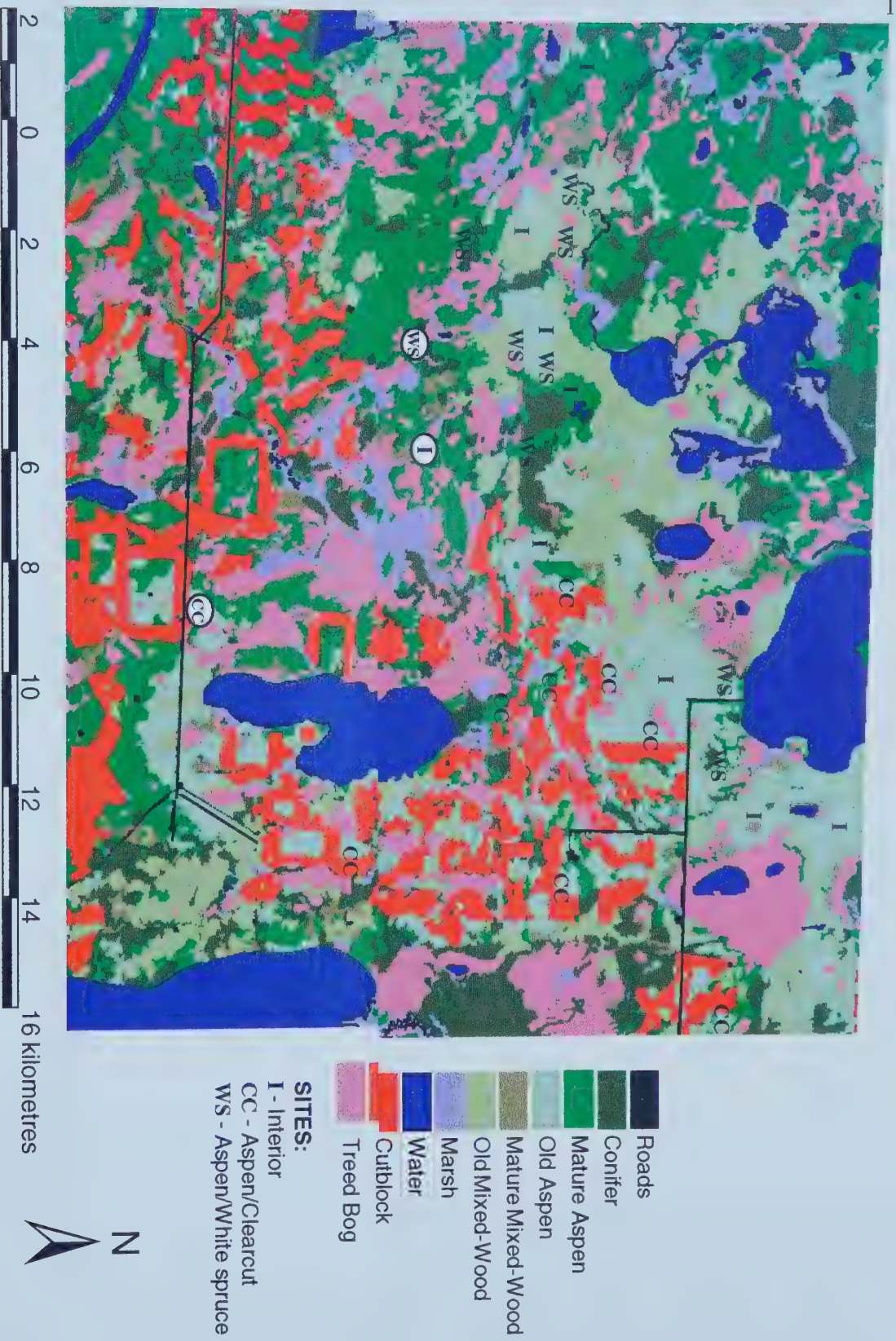

■ Observed □ Expected

Appendix 2.6. continued.

Black-throated Green Warbler - 1995

Black-throated Green Warbler - 1996

Ovenbird- 1995

Ovenbird- 1996

Connecticut Warbler - 1996*

■ Observed □ Expected

Appendix 2.6. continued.

Mourning Warbler - 1995

Mourning Warbler - 1996

White-throated Sparrow - 1995*

White-throated Sparrow - 1996*

Western Tanager - 1995

Western Tanager - 1996

■ Observed □ Expected

145
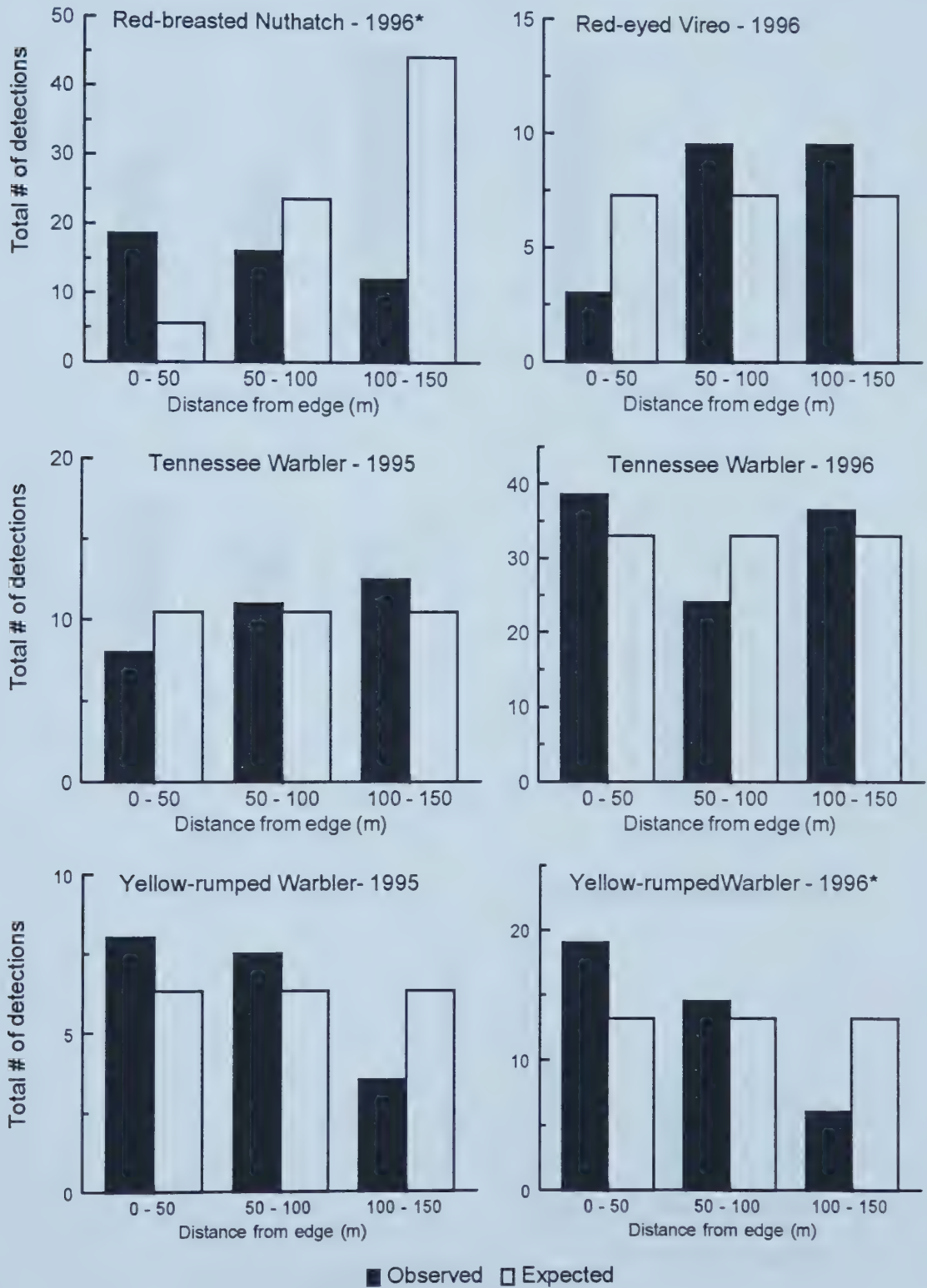
Appendix 3.1 Layout of transects for sampling invertebrates. Circled sites were added in 1996.

SITES:
I - Interior
CC - Aspen/Clearcut
WS - Aspen/White spruce

Roads
Conifer
Mature Aspen
Old Aspen
Mature Mixed-Wood
Old Mixed-Wood
Marsh
Water
Cutblock
Treed Bog

N

2 0 2 4 6 8 10 12 14

16 kilometres

Appendix 3.2. Example of sub-sampling of insect samples to determine sample size. I randomly selected a number of samples along a transect and calculated the standard error. I repeated the procedure five times for each sample size and calculated an average to give the standard error shown on the graph. Standard error reached an asymptote at approximately five samples; therefore, 5 samples were enough to adequately estimate variation within a stand. Samples were collected in 1994.


Sweep net sample

Pitfall trap sample

Number of samples
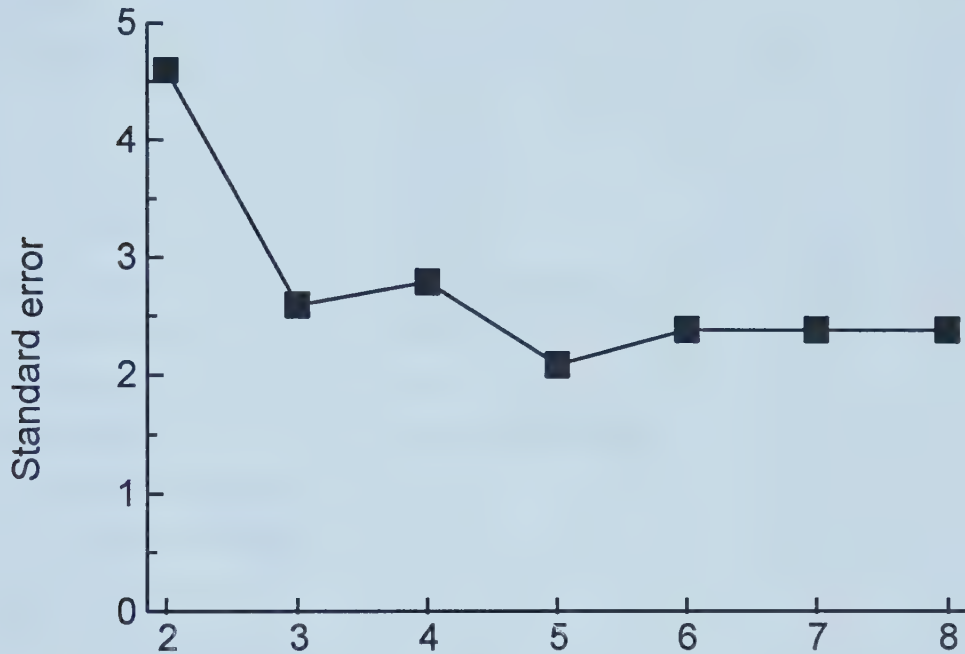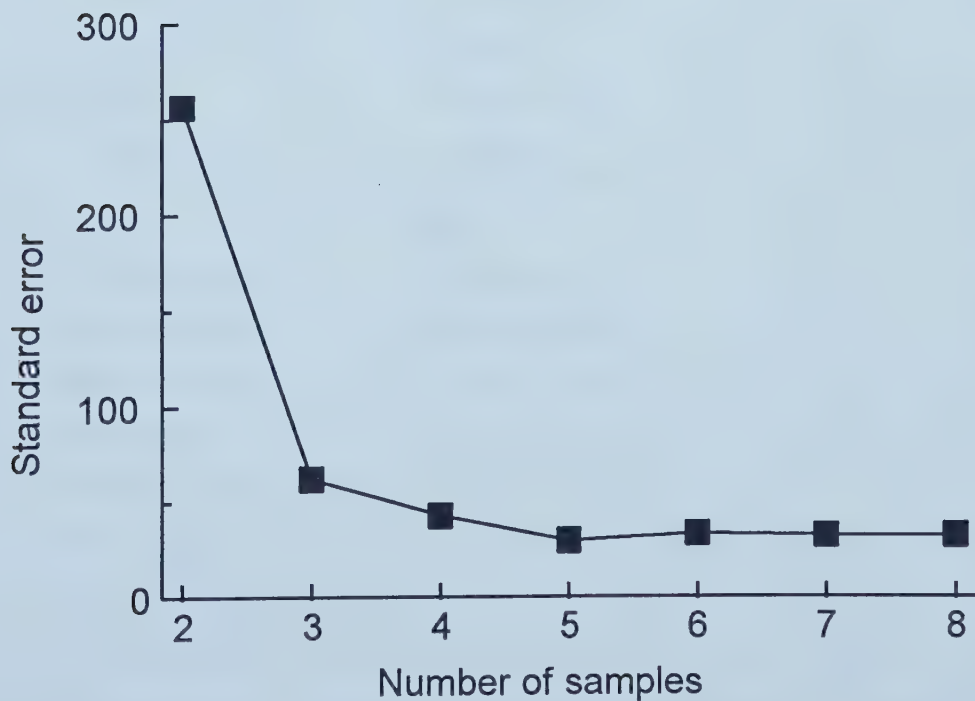
Appendix 3.3. Classification and average biomass/sample of sweep net and pitfall trap captures for 1995-6.

| Classification	Common name	Average biomass (mg)	
		Sweep nets	Pitfall traps
Phylum Mollusca			
Class Gastropoda	Snails & Slugs	0.88	2.03
Phylum Arthropoda			
Class Arachnida	Spiders	4.05	28.67
Class Hexapoda	Insects		
Order Collembola	Springtails	0.06	0.25
Order Psocoptera	Psocids or bark lice	0.03	<0.01
Order Thysanoptera	Thrips	0.01	<0.01
Order Hemiptera	Bugs	0.87	0.58
Order Homoptera	Hoppers, Psyllids, Aphids	5.28	1.51
Suborder Auchenorrhyncha	Hoppers	4.97	1.5
Superfamily Aphidoidea	Aphids	0.25	0.01
Order Neuroptera	Lacewings, etc.	0.15	<0.01
Order Coleoptera	Beetles	5.67	180.46
Family Carabidae	Carabids	<0.01	150.04
Family Staphylinidae	Rove beeetles	0.18	21.57
Family Leiodidae	Round fungus beetles	<0.01	0.48
Order Trichoptera	Caddisflies	0.02	0
Order Lepidoptera	Butterflies & moths	10.7	5.94
Lepidopteran larvae (+ Hym.: Symphyta larvae)	Caterpillars (+ Sawfly larvae)	10.51	5.42
Order Diptera	Flies	9.33	77.04
Suborder Nematocera	Long horn flies	5.07	2.04
Suborder Brachycera	Horse flies, robber flies...	1.11	0.13
Suborder Cyclorrhapha	Heleomyzids, Muscids...	2.99	73.84
Order Hymenoptera	Bees and wasps	1.47	9.13
Suborder Symphyta	Sawflies and horntails	0.6	0.26
Suborder Apocrita			
Family Formicidae	Ants	0.18	3.69
Superfamilies Icneumonoidea, Chalcidoidea, etc.	Parasitic wasps	0.68	0.33
Total mean		38.70	307.27

Appendix 3.4. Size class distribution of mean arthropod biomass per sweep net sample. Black bars represent 1995 and white bars represent 1996. Means are reported +/- SE.
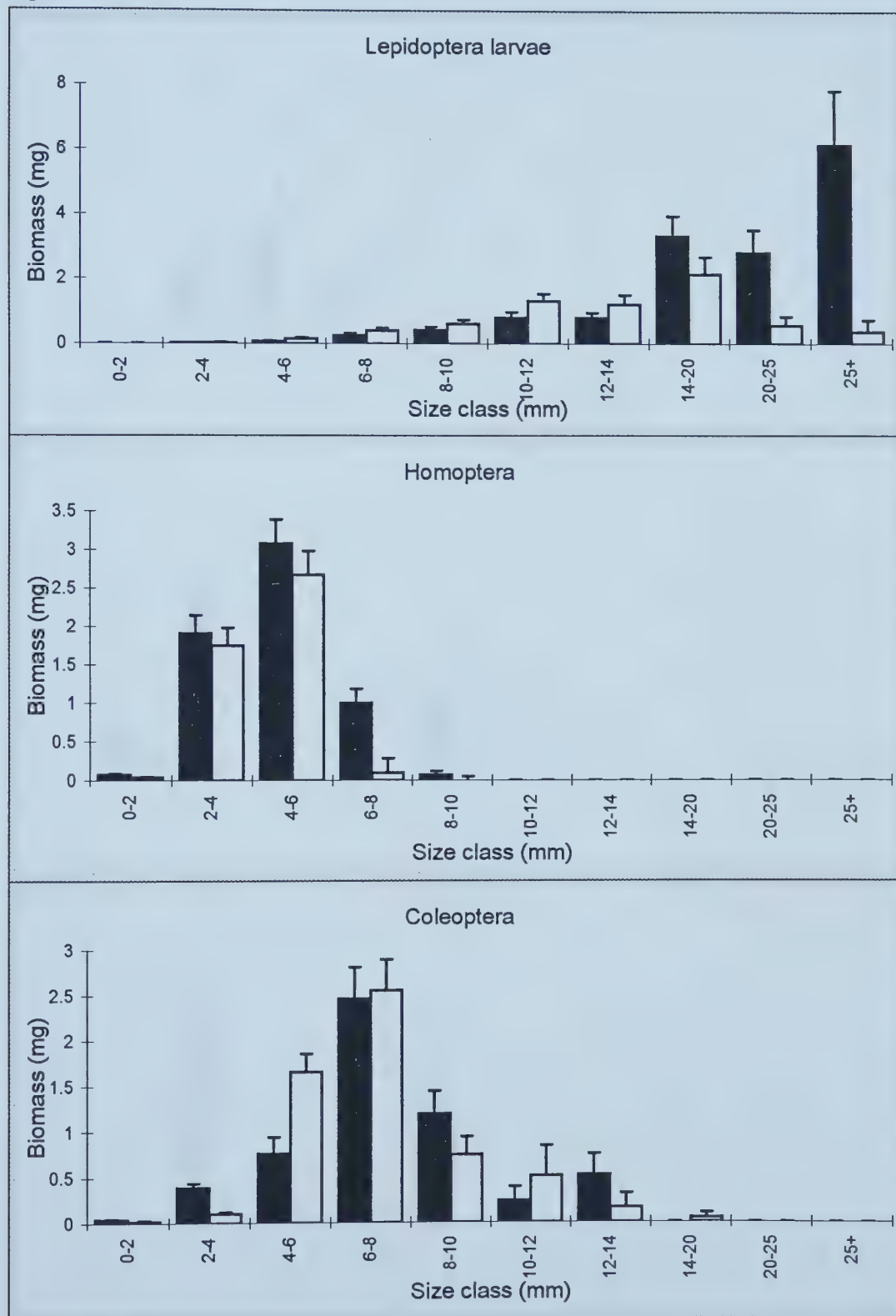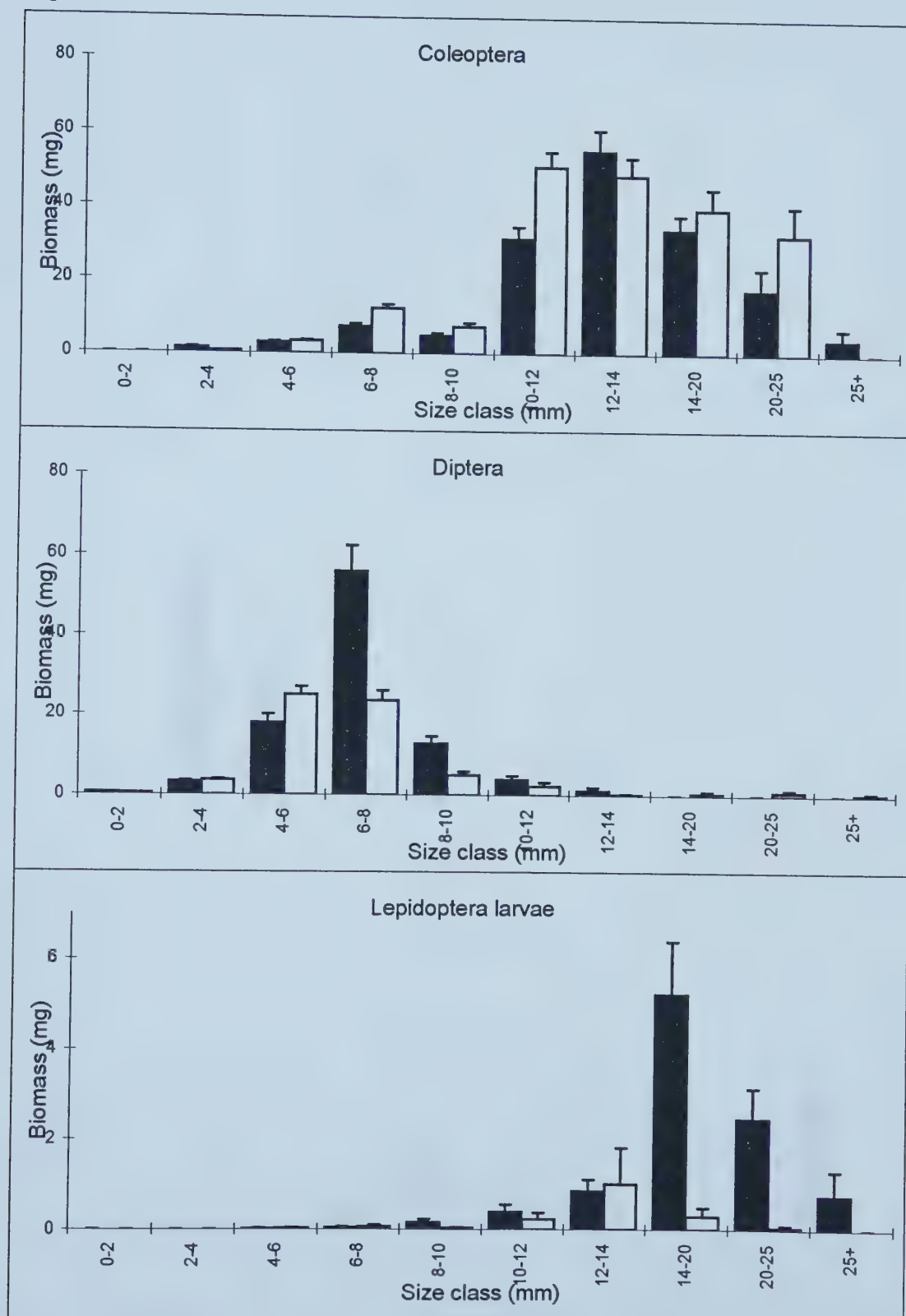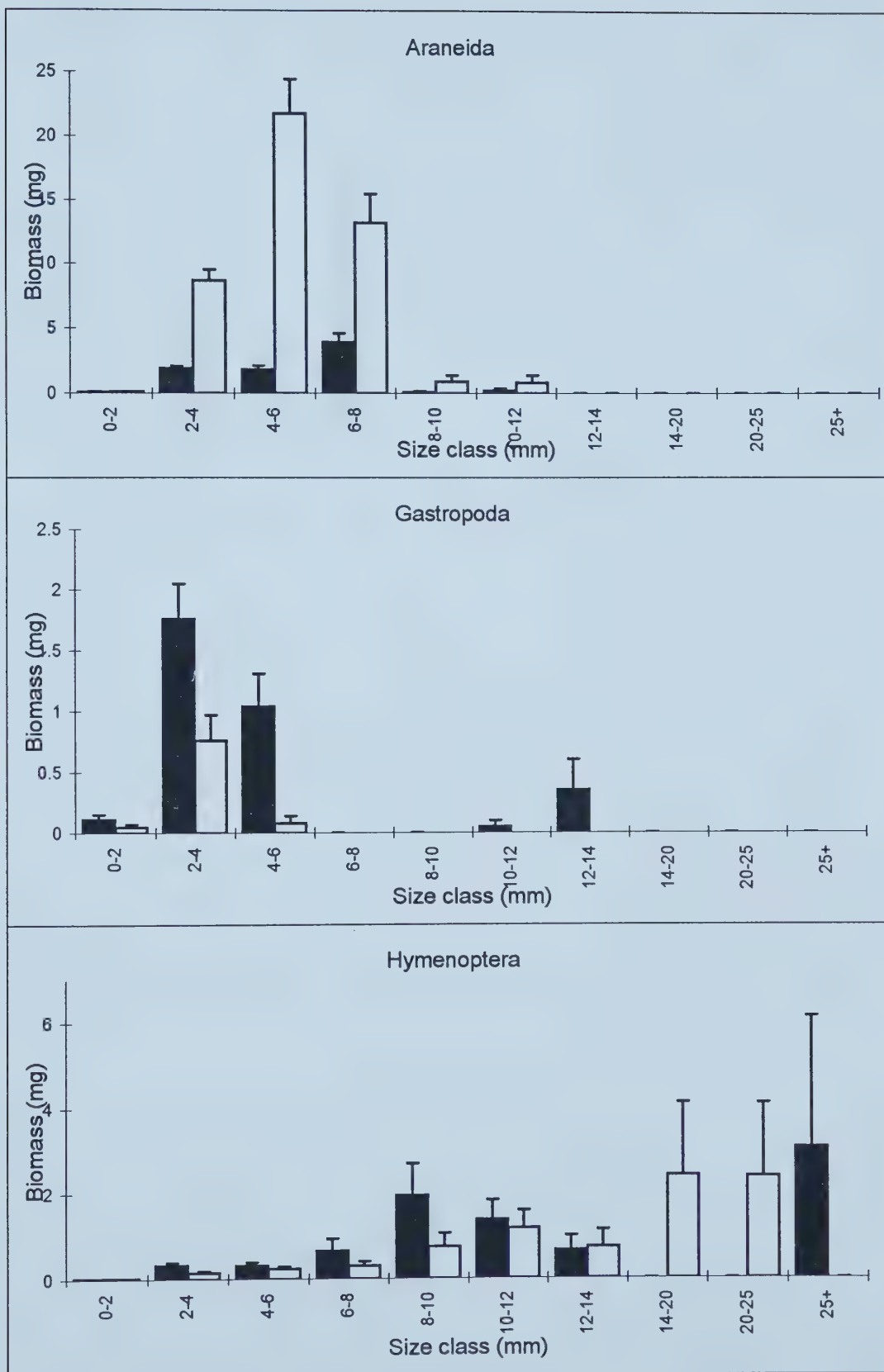
Appendix 3.4. continued.
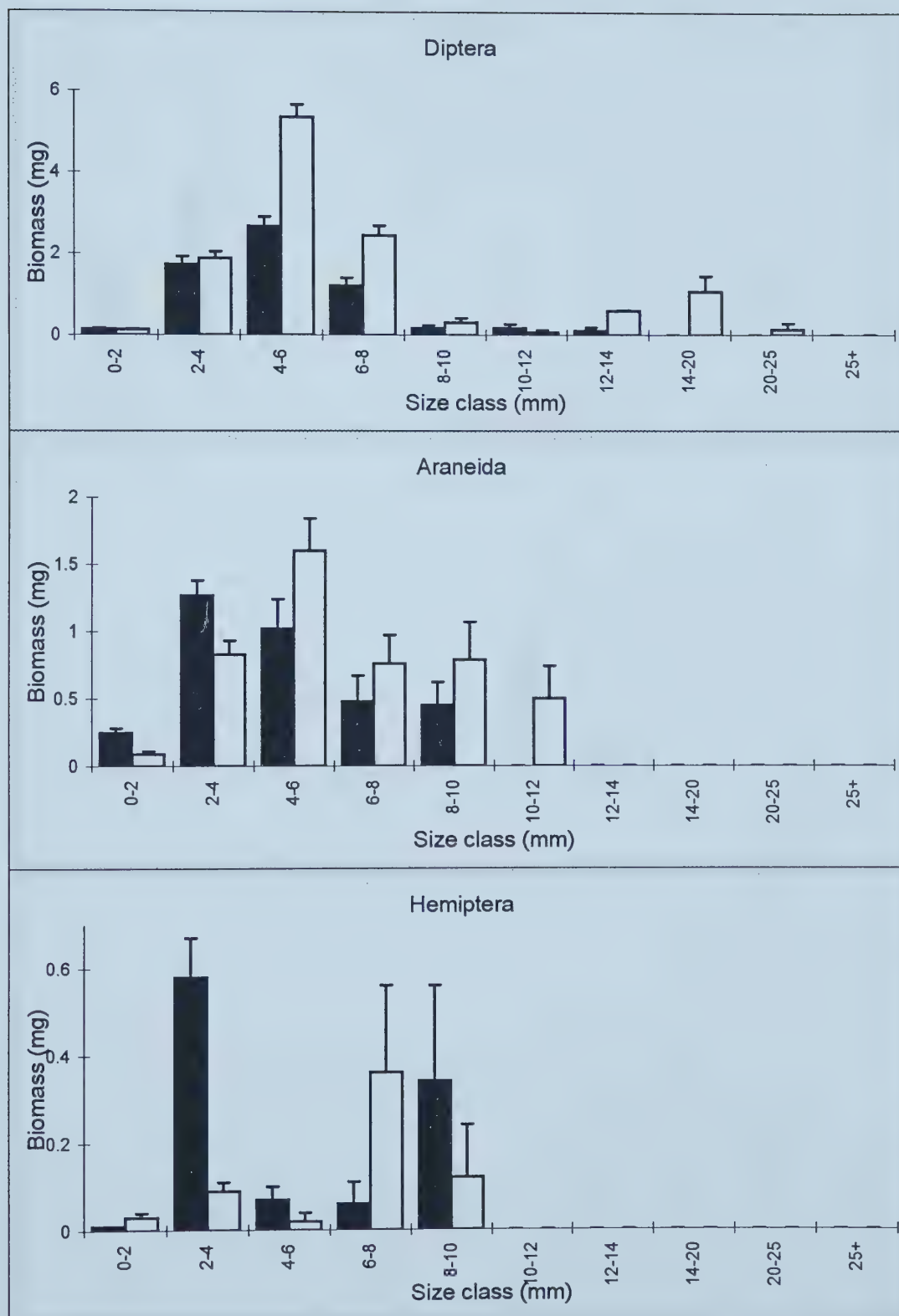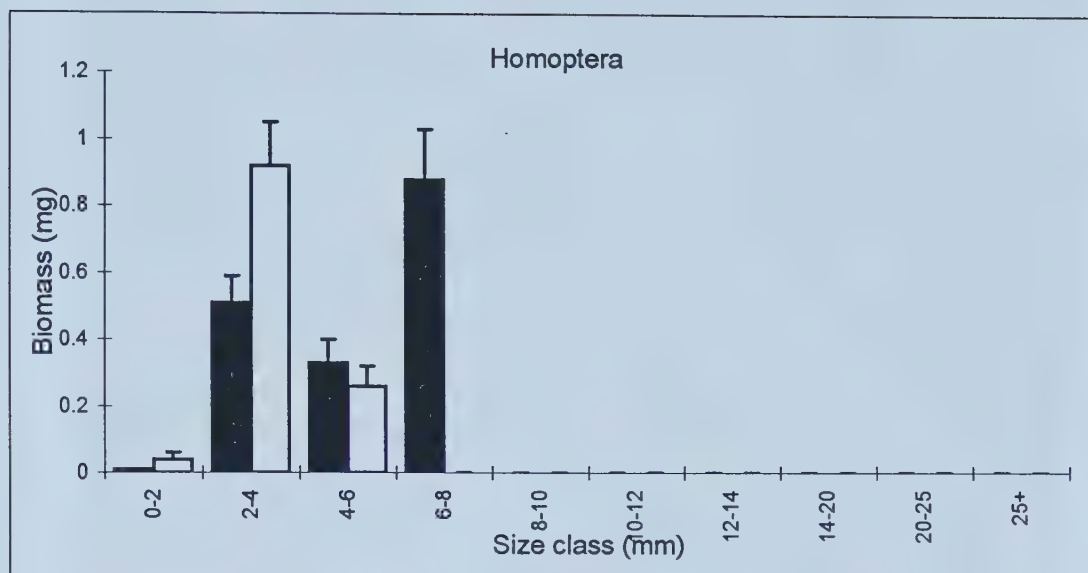
Appendix 3.4. continued.
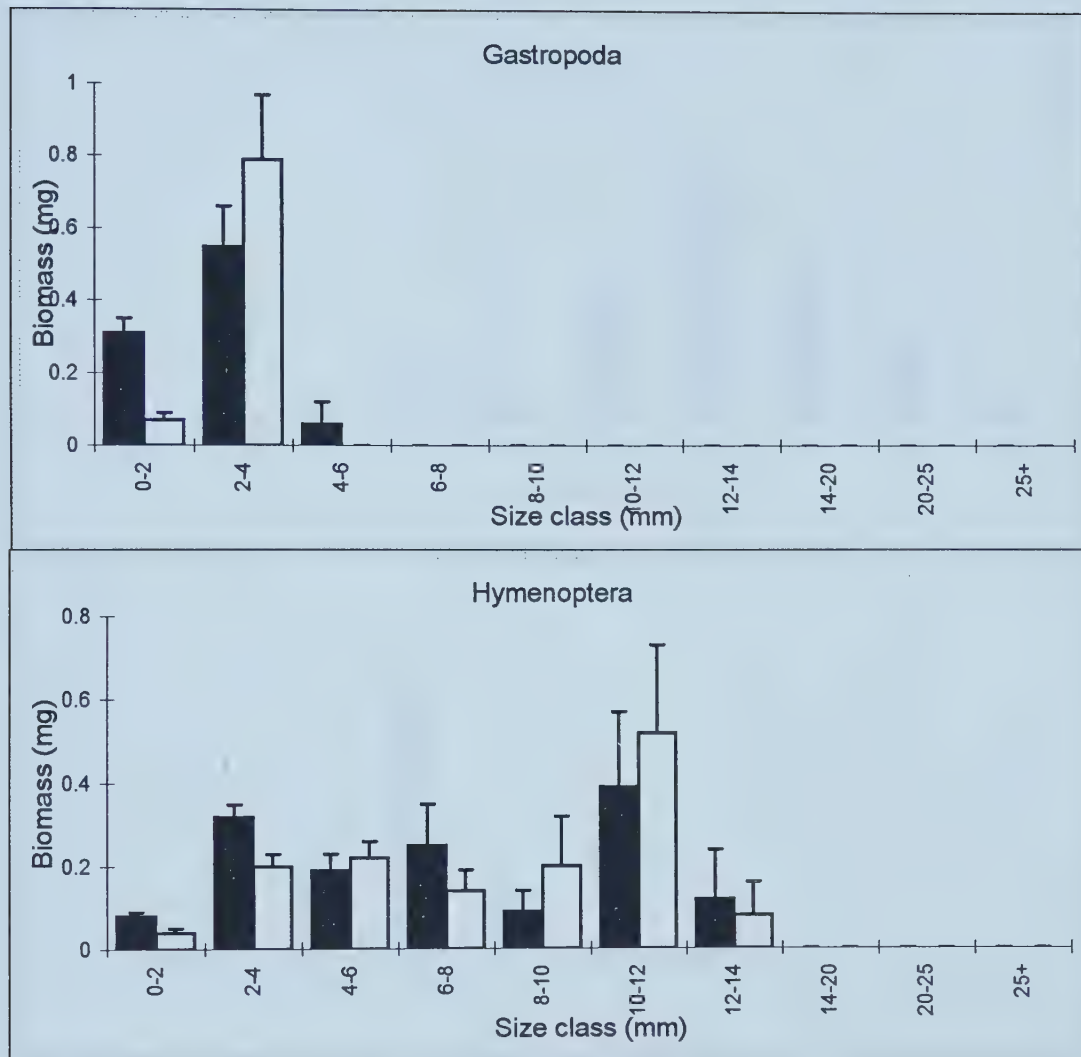
Appendix 3.5. Size class distribution of mean arthropod biomass per pitfall trap sample. Black bars represent 1995 and white bars represent 1996. Means are reported +/- SE
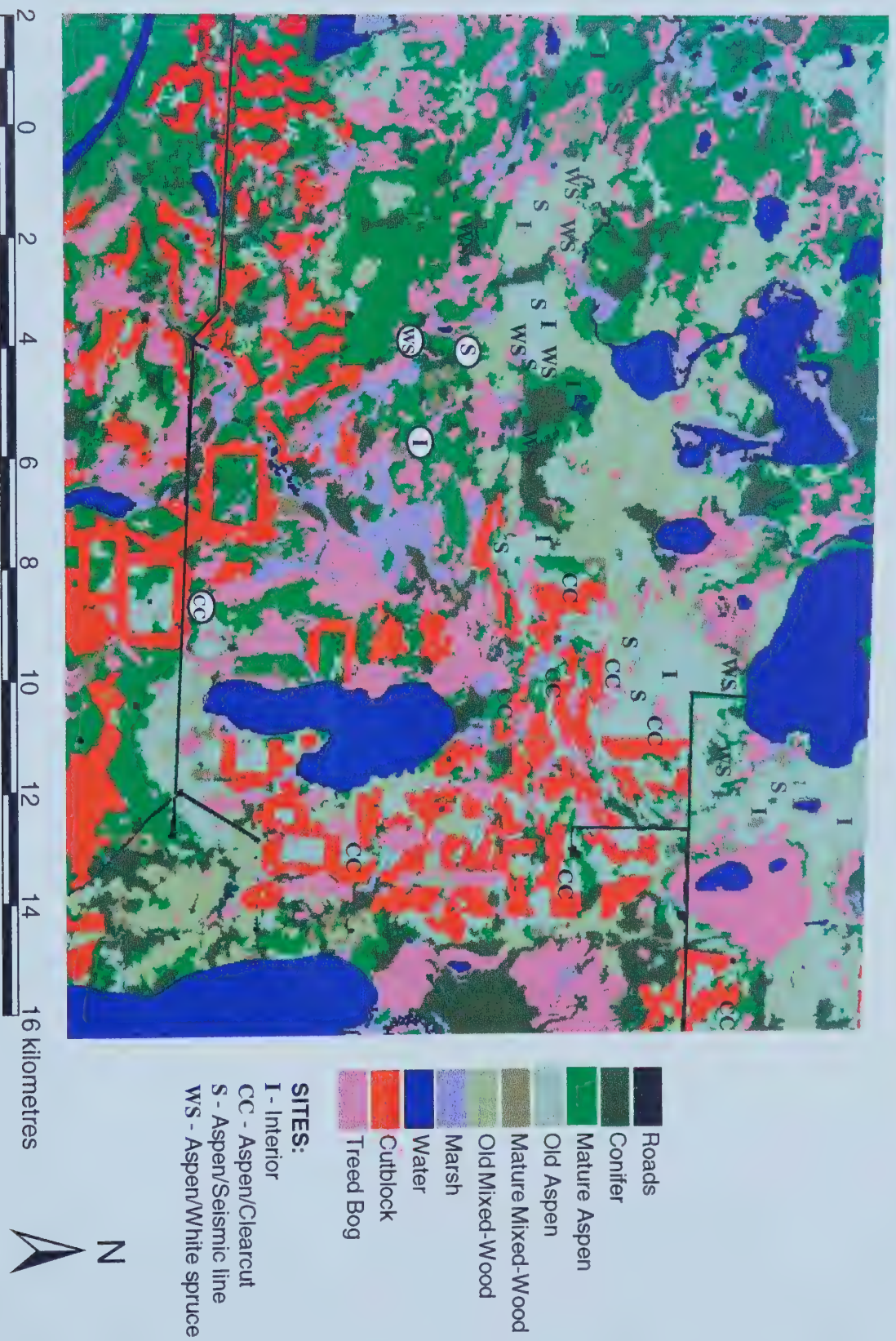
Appendix 3.5. continued.

Appendix 3.5. continued.

Appendix 4.1 Layout of transects for artificial nests. Circled sites were added in 1996.

16 kilometres

N

SITES:
I - Interior
CC - Aspen/Clearcut
S - Aspen/Seismic line
WS - Aspen/White spruce

Roads
Conifer
Mature Aspen
Old Aspen
MatureMixed-Wood
OldMixed-Wood
Marsh
Water
Cutblock
Treed Bog

Appendix 4.2: Loadings for factors generated from PCA on landscape level data.

Radius	Variable	Factor 1	Factor 2	Factor 3
450 m	Bog	0.09585	0.77190	0.38220
	Clearcut	-0.93391	0.08442	-0.28064
	Coniferous forest	0.80192	0.03501	-0.54430
	Aspen forest	0.14673	-0.69449	0.67742
	Water	0.17108	0.61530	0.44285
	Aspen/Coniferous edge	0.80869	0.08759	-0.32483
	Aspen/Clearcut edge	-0.92157	0.10571	-0.24447
250 m	Bog	-0.13634	0.33213	-0.84781
	Clearcut	-0.92579	0.19885	0.14759
	Coniferous forest	0.84882	0.36599	0.05178
	Aspen forest	0.29558	-0.89609	0.09946
	Water	0.22925	0.49016	0.57325
	Aspen/Coniferous edge	0.82322	0.20078	0.04857
	Aspen/Clearcut edge	-0.81513	0.11541	0.27445